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Effect of Discharge Rate on Biotic and Abiotic Chemical Flux in an Acidified Stream

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Hall, R. J., and G. E. Likens. 1984. Effect of discharge rate on biotic and abiotic chemical flux in an acidified stream. Can. J. Fish. Aquat. Sci. 41: 1132–1138.

Acidity of Norris Brook, a mountain stream in the Hubbard Brook Experimental Forest, New Hampshire, was manipulated to estimate the effects on biotic and abiotic chemical flux during high (spring) and low (summer) discharge periods. Sulfuric acid was added to maintain the pH near 4.0 from April to September 1977. Al, Ca, Mg, and K were mobilized into streamwater with concentrations progressively increasing downstream, as a result of increased H^+ concentration. Concentrations of Na and NO_3 were not affected by the acidification. Dissolved organic carbon concentrations decreased downstream during periods of high discharge but did not change significantly during low flow. During storms, Al, Ca, Mg, and K increased in concentration below the acid addition as well as in the reference reach of the stream. Net flux of dissolved Al in streamwater was significant during both high- and low-discharge periods. Net flux of Al in invertebrate biomass was significantly increased only during high flow but was insignificant when compared with the amount in the dissolved form. Net flux of N was significant only in biomass of invertebrates at high discharge. Significance of flux of N in biota was totally overshadowed by transport (flux) of dissolved N (as NO_3 and NH_4) during storms.

On a mené des expériences sur l'acidité du ruisseau Norris, ruisseau de montagne situé dans la Hubbard Brook Experimental Forest (New Hampshire), afin d'évaluer son incidence sur les flux chimiques biotiques et abiotiques pendant les périodes de débit élevé (printemps) et faible (été). On a ajouté de l'acide sulfurique pour maintenir le pH près de 4,0 d'avril à septembre 1977. Al, Ca, Mg et K sont entrés dans le cours d'eau à des concentrations augmentant progressivement en aval, à la suite d'une hausse de la concentration de H^+. Les concentrations de Na et de NO_3 n'ont pas été touchées par l'acidification. Toutefois, celles du carbone organique dissous ont diminué en aval pendant les périodes de débit élevé mais n'ont pas varié significativement pendant les périodes de faible débit. Au cours de tempêtes, les concentrations de Al, Ca, Mg et K ont augmenté en aval du site d'addition d'acide ainsi que dans la partie témoin du cours d'eau. Le flux net de Al dans la biomasse d'invertébrés n'a augmenté de façon marquée que pendant les périodes de débit élevé et était peu important quand on le compare à la quantité sous forme dissoute. Le flux net de N n'était significatif dans la biomasse d'invertébrés qu'à un débit élevé. L'importance du flux de N dans la flore et la faune était complètement cachée par le transport (flux) de N dissous (en NO_3 et NH_4) pendant les tempêtes.

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Dispersal of strong acids in the atmosphere and their deposition on aquatic and terrestrial ecosystems far removed from industrial and urban sources is a well-known phenomenon (Gorham 1958; Oden 1968; Likens et al. 1979; Schofield 1972; Summers and Whelpdale 1976). Acidification of freshwater lakes and streams as a result of accelerated atmospheric deposition of H^+ has been reported in Scandanavia (Overrein et al. 1980), in the Canadian Shield (Beamish and Harvey 1972; Dillon et al. 1980), and in the northeastern United States (Likens et al. 1979; Schofield 1976). Because these geographic regions are generally underlain by siliceous bedrock highly resistant to chemical weathering, they have poorly buffered surface waters (Schofield 1972; Wright and Henriksen 1978; Likens et al. 1979) susceptible to pH depression resulting from inputs of atmospheric H^+.

Studies by investigators concerned with the stress from H^+ have been either field surveys, in which changes in species composition at different trophic levels have been correlated with low pH (Sutcliffe and Carrick 1973; Almer et al. 1974; Raddum 1980), or physiological laboratory studies, in which alteration of the internal ionic balance for fish and invertebrates at low pH has been determined (Muniz and Leivestad 1980; Havas 1981). However, changes in chemical flux in biotic and abiotic

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components and in the ability of natural aquatic ecosystems to neutralize acidic inputs are poorly understood quantitatively. Another problem in aquatic ecosystems stressed by strong acid is the difficulty of differentiating between causal effects of natural biogeochemical change in H^+ concentration and man-made pH stress (Cooper 1978). In 1977, Hall et al. (1980) conducted a comprehensive study of various qualitative and quantitative changes in the biology and geochemistry of an experimentally acidified stream. A series of field experiments tested the general hypothesis that such acidification would alter the stream chemistry (Hall and Likens 1981) and adversely affect the biota (Hall et al. 1982; Pratt and Hall 1981) inhabiting Norris Brook, a small woodland mountain stream within the Hubbard Brook Experimental Forest, New Hampshire.

This paper focuses on the abiotic and biotic spatial changes in chemical flux as a result of H^+ stress. Our intent was to show that chemical flux is a function of stream discharge as well as stream acidification. We are unaware of any investigators who have attempted to compare the effect of increased acidity on ecosystem metabolism and biogeochemistry during high and low flow, particularly during rain storms. Other acid-induced changes concerning water chemistry, drift, macrobenthic communites, periphyton, and fish are presented elsewhere (Hall and Likens 1980, 1981; Hall et al. 1980, 1982).

Study Site

The experimental reach of Norris Brook was located on a third-order stream. The watershed soils are mostly well-drained spodosols of sandy loam texture with 3–15 cm organic layer at the surface (Likens et al. 1977). Soil depths average about 0.5 m from surface to bedrock or till.

Stream discharge at the Hubbard Brook Experimental Forest is quite variable by season (Likens et al. 1977). Most of the annual streamflow occurs in spring during snowmelt, with 54% of it occurring during March, April, and May and more than 30% in April alone. During summer months, streamflow is very low, particularly during August and September, but a smaller peak due to somewhat more rainfall and decreased transpiration occurs in November and December. Winter discharge is reduced as precipitation accumulates in a snowpack.

Changes in mean daily streamwater discharge, corresponding to rainfall events, occurred frequently and were distributed somewhat evenly throughout the experimental period (18 April–22 September; see Hall et al. 1980 for weekly discharge values). During the six largest storms, mean daily discharge was 24.2 L/s; 14 smaller storm events produced a mean daily discharge of 2.7 L/s.

We divided our results into high-discharge (18 April–31 May) and low-discharge (1 June–22 September) periods. Mean daily baseflow (peaks excluded) during the experiment was 8.3 L/s (range 0.25–12 L/s, $N = 40$) in spring (18 April–31 May) and 1.06 L/s (range 0.05–5.2 L/s, $N = 100$) during summer and early autumn (1 June–22 September).

Materials and Methods

The experimental design and methods for chemical and biological analyses are detailed elsewhere (Hall et al. 1980). Only those methods and procedures not described previously are given here.

Dilute sulfuric acid (0.5–1.0 mol/L) was added manually to the stream from a 190-L polyethylene container for 5 mo. Each carboy of concentrated acid (36 mol/L) was diluted with Norris Brook water, and then this acid solution was added continuously to the stream. Water samples for chemical analysis were collected 2 m above (site A) and at four stations 15, 30, 75, and 100 m below acid addition.

To determine water quality during two heavy rainstorms in August and September, we collected streamwater samples at all stations at 6- to 8-h intervals at the onset of rainfall (stream discharge at baseflow), through the rapid increase in stream discharge, and through subsidence.

Invertebrate drift samples were collected at sites A and B over 24-h periods. Estimates of flux of Al and N in streamwater and invertebrate biomass were determined by differences between input from the upstream reference area (site A) and output below the acid addition point (site B). We chose Al because (1) it is toxic to fish (Schofield 1976; Cronan and Schofield 1979; Driscoll et al. 1980) and possibly other aquatic organisms (Hall et al. 1984) and (2) the solubility of Al minerals is a function of pH and thus is a partial indication of H^+ neutralization (Driscoll et al. 1980; Johnson et al. 1981). Nitrogen was chosen because it is an essential nutrient for stream biota. Flux (milligrams per day) of these ions by streamwater at sites A and B was calculated as the product of chemical concentration (milligrams per litre) and discharge (litres per day). Estimates of chemical concentration in invertebrate biomass (dry mass) in reference and treatment sections for the 1977 acidification experiment were determined as the product of chemical concentration in invertebrates (milligrams per gram) found in drift nets during the summer of 1978 and the biomass that drifted (grams per day). The chemical analysis of invertebrates was not determined in 1977.

Results

Several observed changes in water chemistry can be attributed to seasonal fluctuations in stream discharge, to experimental acidification, or to a combination of both. Concentrations of Al, Ca, Mg, K, Na, and dissoved organic carbon (DOC) were lowest during high-flow (Table 1, site A) relative to low-discharge periods. Below the point of acid addition, Al, Ca, K, and Mg were mobilized in streamwater (relative to the reference area) with concentrations progressively increasing downstream; H^+ decreased downstream (Table 1). After acidification, DOC concentration decreased significantly during high but not during low flow, and Na concentrations remained unchanged. During rain storms, Al, Ca, K, and Mg were mobilized in the acidified reach to an even greater extent, DOC concentration increased, and Na concentration decreased (Tables 2 and 3). In the reference area, pH dropped from 6.1–6.4 at low discharge rates (0.8–0.9 L/s) to 5.5 at high discharge (22.8–52 L/s) during rain storms (Tables 2 and 3).

Mean daily concentrations of Al dissolved in streamwater during high discharge were 0.03 ± 0.006 and 0.05 ± 0.008 mg/L at sites A and B, respectively, with a net flux of -0.02 mg/L; during low discharge the concentrations were 0.08 ± 0.007 and 0.12 ± 0.008 mg/L at sites A and B, respectively, with a net flux of -0.04 mg/L. Mean daily concentrations of NH_4 dissolved in streamwater during high discharge was 0.01 ± 0 mg/L for both reference and treatment areas (net flux = 0); during low discharge the concentration was 0.004 ± 0.003 mg/L at both sites (net flux = 0). Nitrate concentrations were undetectable. Mean daily invertebrate biomass during high

TABLE 1. Mean (±SE) concentrations (mg/L) of dissolved elements and pH in streamwater and di
acidified sites (B-15m, C-30m, D-75m, and E-100m) for high (18 April–31 May) and low (1 June–
DOC for high discharge; $N = 15$ and 11, respectively, for low discharge. Samples were taken at the
2 d, and every 24 h for the next 3 d. Thereafter, samples for chemical analysis were taken at week

	High-discharge period				
	A	B	C	D	E
pH	6.15±0.046	4.0±0.010	4.03±0.0069	4.08±0.044	4.16±0.074
Al	0.033±0.007	0.057±0.008***	0.068±0.007***	0.089±0.008***	0.096±0.008*
Ca	1.69±0.016	1.69±0.016	1.75±0.019***	1.80±0.022***	1.87±0.029*
Mg	0.36±0.004	0.36±0.004	0.36±0.005	0.37±0.004***	0.38±0.005*
K	0.26±0.01	0.26±0.01	0.26±0.01	0.27±0.01***	0.27±0.01**
Na	1.0±0.05	1.0±0.05	1.0±0.05	1.0±0.05	1.0±0.05
NO_3	0	0	0	0	0
NH_4	0.01	0.01	0.01	0.01	0.01
DOC	1.92±0.165	—	—	—	1.45±0.079*

TABLE 2. Concentration of dissolved ions (mg/L) and pH during a storm event (16–
16 August) and during the rising (03:00, 17 August) and falling (09:00, 17 August)
D-75m, and E-100m) acid addition.

	A			B				
Discharge (L/s)	0.90 (12:00)	22.8 (03:00)	4.6 (09:00)	0.90 (12:00)	22.8 (03:00)	4.6 (09:00)	0.90 (12:00)	(
pH	6.4	5.5	6.0	4.0	3.95	4.0	4.1	
Al	0.12	0.84	0.38	0.14	0.72	0.43	0.20	
Ca	2.02	2.79	2.7	2.1	2.84	2.72	2.34	
Mg	0.49	0.63	0.60	0.51	0.64	0.61	0.54	
K	0.27	0.54	0.38	0.28	0.55	0.38	0.29	
Na	1.84	1.47	1.47	1.85	1.48	1.50	1.86	
NO_3	<0.01	0.48	<0.01	<0.01	0.50	<0.01	<0.01	
NH_4	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<
DOC	3.4	8.9	7.1	3.2	12.2	7.1	2.9	

er and differences between means tested by Student's *t*-test for paired samples in reference (site A) and (1 June–22 September) discharge periods. $N = 13$ for dissolved ions (i.e. pH through NH_4) and 11 for en at the five sites every 6 h during the first 2 d of the experimental acidification, every 12 h for the next at weekly intervals. $^*p < 0.05$; $^{**}p < 0.005$; $^{***}p < 0.005$.

	Low-discharge period				
E	A	B	C	D	E
±0.074	6.3±0.025	4.0±0.011	4.08±0.017	4.19±0.032	4.25±0.042
±0.008***	0.09±0.012	0.12±0.008**	0.14±0.010***	0.17±0.011***	0.17±0.011***
±0.029***	1.99±0.024	2.04±0.019	2.1±0.044**	2.17±0.052***	2.24±0.051***
±0.005***	0.46±0.008	0.47±0.007**	0.48±0.009*	0.48±0.018*	0.49±0.011*
±0.01***	0.31±0.015	0.31±0.016	0.33±0.017**	0.35±0.021***	0.35±0.019***
±0.05	1.61±0.068	1.62±0.064	1.62±0.064	1.61±0.063	1.61±0.058
0	0	0	0	0	0
0.01	0.01	0.01	0.01	0.01	0.01
±0.079*	3.23±0.233	—	—	—	3.05±0.180

ent (16–17 August 1977). Samples were collected before increased discharge (12:00, August) discharge hydrograph above (site, A, 2 m) and below (sites B-15m, C-30m,

C			D			E		
90 :00)	22.8 (03:00)	4.6 (09:00)	0.90 (12:00)	22.8 (03:00)	4.6 (09:00)	0.90 (12:00)	22.8 (03:00)	4.6 (09:00)
.1	4.0	4.1	4.25	4.0	4.16	4.35	4.1	4.2
.20	0.56	0.40	0.24	0.46	0.41	0.25	0.39	0.40
.34	2.88	2.84	2.43	2.97	2.88	2.56	3.03	2.9
.54	0.64	0.63	0.55	0.65	0.63	0.56	0.65	0.64
.29	0.57	0.40	0.31	0.57	0.40	0.32	0.59	0.40
.86	1.47	1.50	1.84	1.47	1.50	1.85	1.46	1.50
.01	0.48	<0.01	<0.01	0.50	<0.01	<0.01	0.48	<0.01
.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
.9	9.5	6.0	3.1	9.5	6.0	3.2	9.3	6.0

discharge was 0.06 ± 0.007 and 0.16 ± 0.039 g/d at sites A and B, respectively, with a net flux of −0.10 g/d; during low discharge, biomass was 0.018 ± 0.007 and 0.019 ± 0.007 g/d at sites A and B, respectively, with a net flux of −0.001 g/d. Insects contained 0.84 mg Al/g dry mass and 75 mg N/g dry mass.

Amounts of transported dissolved inorganic Al per day in both reference and treatment areas were greater than the amounts of Al in invertebrate biomass (Table 4; for invertebrate species composition in drift collections, see Hall et al. 1980; Pratt and Hall 1981; Hall et al. 1982). A significant increase in amount of dissolved Al occurred as a result of acidification during high (Student's t, $p < 0.0005$; 125% increase) and low ($p < 0.025$; 17% increase) flow. Transport of Al in invertebrate biomass out of the treatment area during high flow was significant ($p < 0.01$; 170% increase; mainly due to differences in biomass fluxes between sites A and B) relative to Al that moved into the treatment area (site A); no significant ($p > 0.3$; 5% increase) loss of Al in invertebrates occurred during the low-flow period. Net mean flux of dissolved Al was greater during high-flow than during the low-discharge period. Net daily flux of Al in invertebrate biomass was considerably smaller than that for dissolved Al during both high- and low-discharge periods.

In contrast with Al, net flux of N in invertebrate biomass was greater than net flux in the dissolved state during the experiment (Table 4). Net flux of dissolved N for both high- and low-flow periods was undetectable. Net flux of N in the biomass of invertebrates increased 168% ($p < 0.025$) and 5% ($p > 0.3$) during high and low discharge, respectively, relative to site A (Table 4).

In summary, net fluxes of Al and N out of the experimental reach during high-flow periods in the spring were greater than those during low-discharge periods in summer and early autumn. Under H^+ stress, net flux of Al was much greater in the dissolved than the invertebrate biomass phase. In contrast, net flux of N was greater in invertebrate biomass than in the dissolved phase. The pH in the reference area was reduced approximately one unit (6.4 to 5.5) during elevated discharge.

Discussion

Many of the temporal and spatial gradients in streamwater chemistry resulted from changes in hydrology alone, such as mixing of surface runoff (i.e. snowmelt and/or rainstorms) with deeper soil water (Johnson et al. 1969; Kirkby 1978; Hall et al. 1980; Reid et al. 1981) and within-stream disturbance (Casey and Farr 1982). Superimposed upon hydrologic patterns, however, were effects due to experimental acidification. Presumably, cation increases as a result of H^+ addition may have resulted from dissolution of aluminum hydroxide compounds (Cronan and Schofield 1979; Johnson 1979; Driscoll et al. 1980; Johnson et al. 1981), or by cation exchange on sediment exchange sites (Reid et al. 1981; Dillon et al. 1984), or by chemical weathering reactions on stream bank soils (Likens et al. 1977; Reid et al. 1981), or some combination of these mechanisms. Mobilization of Al, Ca, and Mg has been observed in watersheds that receive large amounts of H^+ from ambient precipitation in southern Norway (Gjessing et al. 1976; Henriksen and Wright 1977), southern Sweden (Wright et al. 1980), southwestern Scotland (Wright et al. 1980), northeastern Scotland (Reid et al. 1981), the White Mountains of New

TABLE 3. Concentration of dissolved ions (mg/L) and pH in streamwater during a storm event (13–14 September 1977). Samples were collected before increased discharge (12:00, 13 September) and during the rising (19:00, 13 September and 04:00, 14 September) and falling (13:00, 14 September) discharge hydrograph for reference (site A, 2 m above) and acidified areas (sites B-15m, C-30m, D-75m and E-100m below acid addition).

	A				B				C				D				E			
Discharge (L/s)	0.8 (12:00)	12 (19:00)	52 (04:00)	26 (13:00)	0.8 (12:00)	12 (19:00)	52 (04:00)	26 (13:00)	0.8 (12:00)	12 (19:00)	52 (04:00)	26 (13:00)	0.8 (12:00)	12 (19:00)	52 (04:00)	26 (13:00)	0.8 (12:00)	12 (19:00)	52 (04:00)	26 (13:00)
pH	6.1	6.0	5.5	5.8	4.01	4.0	4.0	4.1	4.2				4.4				4.5	4.1	4.1	4.1
Al	0.11	0.28	0.33	0.15	0.12	0.26	0.42	0.16	0.14				0.16				0.14	0.27	0.42	0.19
Ca	2.05	2.39	2.45	2.29	2.12	2.38	2.54	2.32	2.16				2.16				2.25	2.49	2.69	2.50
Mg	0.50	0.54	0.49	0.47	0.51	0.54	0.50	0.47	0.52				0.50				0.51	0.55	0.51	0.49
K	0.45	0.74	0.49	0.20	0.49	0.74	0.50	0.29	0.50				0.53				0.53	0.76	0.51	0.30
Na	1.84	1.66	0.96	0.99	1.85	1.66	0.97	1.01	1.84				1.82				1.80	1.66	0.97	1.02
NO_3	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
NH_4	<0.01	0.03	0.04	<0.01	0.01	0.03	0.03	<0.01	<0.01			<0.01	<0.01			<0.01	<0.01	0.03	0.06	<0.01

TABLE 4. Mean daily (±SE) chemical amounts and fluxes (mg/d) of Al and N moving into (site A) and out of (site B) the acidified area in streamwater (dissolved) and invertebrates during high-discharge (18 April–31 May) and low-discharge (1 June–22 September) periods.

	High discharge						Low discharge					
	Dissolved (mg/day)			Invertebrates (mg/day)			Dissolved (mg/day)			Invertebrates (mg/day)		
	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N
Al												
Site A	16 000	3215	11	0.049	0.006	11	77 000	39 000	7	0.0156	0.005	7
Site B	36 000	6670	11	0.132	0.03	11	90 000	43 000	7	0.0164	0.006	7
Net flux	−20 000			−0.117			−13 000			−0.0008		
N												
Site A	<8 000[a]	1120	11	4.4	0.535	11	<5 000[a]	3 000	7	1.38	0.523	7
Site B	<8 000[a]	1120	11	11.8	4.42	11	<5 000[a]	3 000	7	1.45	0.521	7
Net flux	0			−7.4			0			−0.07		

[a]Only NO_3 and NH_4 concentrations from Table 1, not from samples taken frequently from storms (Tables 2 and 3), were used to compute fluxes.

Hampshire (Driscoll and Likens 1982), and southeastern Ontario (Dillon et al. 1980).

The increased streamwater concentrations of NO_3 NH_4, and DOC during the ascending limb of the storm hydrograph (Tables 2 and 3) may be due to some combination of direct rainfall on the stream and subsurface flow (Dunne 1978; Sloane 1979; see Kirkby 1978) along stream banks, while Al concentrations are probably augmented by the latter process. Overland flow is negligible within the Hubbard Brook Experimental watershed (Pierce 1967; Likens et al. 1977). DOC and total Al had higher concentrations in groundwater seeps than in streamwater during summer in a second-order reach of Bear Brook (Mulder 1980). Tate and Meyer (1983) and Meyer and Tate (1983) reported that stream DOC export was underestimated by 35% by not considering DOC concentrations during storms. Sloane (1979) usually measured increases in NO_3-N in streams during storms at Hubbard Brook during 1977. She recorded a high NO_3 concentration of 0.5 mg/L during one storm in July as an anomaly. However, we measured a similar concentration (Table 2) in Norris Brook. In addition, the high mean NO_3 concentrations that Sloane measured in groundwater seeps during August (0.28 mg/L) and September (0.43 mg/L) could have contributed to increased concentrations in streamwater during storm flow. A critical factor in the determination of dissolved N, DOC, and Al transport in the stream during storms, thus, is the time at which samples are taken over the course of the storm hydrograph (see Casey and Farr 1982). Other substances, such as P (Meyer 1978; Meyer et al. 1981; Casey and Farr 1982), fine particulate matter (Bilby and Likens 1979; Emmett 1978), and Fe and Mn (Reid et al. 1981), are also transported in streamwater at larger concentrations during rapidly increasing discharge following rainstorm events (within 3–5 h).

The significant decrease in DOC concentrations in acidified streamwater relative to the reference area during the high-discharge period may be explained by binding of increased dissolved Al and DOC, followed by precipitation from the water column. Dickson (1975) determined in laboratory experiments with poorly buffered acidified water (pH 4–5) that suspended humic material precipitated in the presence of Al, but not in buffered acidified water. Lakes in Sweden that have been acidified and exposed to elevated Al concentrations have very clear water (Almer et al. 1978).

The increased concentrations of some cations following acidification occurred over much shorter lengths of stream during low flow. For example, dissolution of Mg and K was not significant at sites B (15 m) and C (30 m) during high flow, but Mg concentrations were significantly elevated in the water at sites B and C, and K concentrations at site C, during low flow conditions (Table 1). Presumably more contact time existed between streambed and acidified streamwater during low- than high-flow periods, resulting in increased dissolution of these basic cations over a shorter distance. On the other hand, Al was significantly elevated at all experimental sites relative to site A, and Ca was mobilized at sites C, D, and E during both high and low flow. If we assume that our experiment represents characteristics of a longitudinal gradient in water quality in streams draining watersheds that receive H^+ from an external source (i.e. incident precipitation or experimental addition of H^+), then our results fit the two-step H^+ neutralization process described by Johnson (1979) and Johnson et al. (1981). As H^+ is added to streamwater, Al dissolution reactions initially neutralize these mineral acids, yielding streamwater with considerable Al acidity. As the water progresses downstream, Al acidity and the remaining H^+ acidity are neutralized by cation exchange reactions and by kinetically slower dissolution of primary minerals. The longitudinal gradient in cation concentrations provides evidence that the rate of neutralization is limited by dissolution kinetics of minerals within stream systems. Further evidence for limited dissolution reactions on the stream bottom is provided by the observation that H^+ neutralization (pH rise) occurred much farther downstream during high-flow (400 m; see Fiance 1979) than during low-flow conditions (50 m, Table 1). As streamflow increases, sediment–H^+ contact time decreases, while mineral dissolution rates remain constant. As a result, the distance over which mineral dissolution occurs is lengthened.

Significant amounts of N were lost from the acidified reach in biomass of invertebrates, particularly during high flow (but not in the dissolved state). Otherwise, this nutrient is conserved during spring and summer baseflow in undisturbed, forest stream ecosystems in the White Mountains of New Hampshire (Likens et al. 1977). Significant amounts of P, organic C, and S also were lost in invertebrate biomass at pH 4.0 relative to streamwater at pH 6.5, and the daily loss of these three elements in invertebrates was greater during early spring (Hall and Likens

1981). However, dominant cations other than Al (i.e. Ca, Mg, K, and Na) did not increase in proportion to the flux of N at site B (see Hall and Likens 1981, table 1).

Although a significant net flux of N occurred in the biota because of H^+ stress during the high-discharge period (Table 4), more N transport as NO_3 or NH_4 occurred in the dissolved phase during stormflow (Tables 2 and 3). Because floods are conspicuous features in most stream systems, the net flux of N in biomass of biota due to elevated acidity decreases in importance. Furthermore, the flux associated with large and fine particles (organic and inorganic) (see Hall and Likens 1981) has not been included here, and if it had, the proportion of invertebrate drift to total flux would have been even smaller.

Our data show the importance of high-discharge periods. Larger concentrations of Al and N were exported to downstream reaches during these periods. Not included in our estimate of biologic flux of N were the trout, sculpins, frogs, and salamanders we collected in drift nets in the acidified section. Thus, the value for N flux in biota is underestimated. In addition, we determined that concentrations of cations are dilute during high discharge in spring relative to concentrations during low flow. Therefore, high-discharge periods are very important to function of stream ecosystems because (1) organisms appear to be more susceptible to high acidity when cation concentrations are low, (2) as much as 58% of the annual streamwater runoff occurs between March and May at Hubbard Brook (Likens et al. 1977), and (3) the net chemical flux of Al and N was greatest during high flow.

The snowmelt period is a critical event in which increased H^+ stress may occur in streams. For example, input of H^+ during spring snowmelt caused the pH to drop to nearly 4.0 in first- to third-order streams in the Adirondack Mountains, New York (Schofield 1977). Jeffries et al. (1979) reported significant pH depressions in lakes and streams in central Ontario during snowmelt. Johannessen and Henriksen (1978) determined from laboratory and field experiments in Norway that 50–80% of acidic materials (H_2SO_4 and HNO_3) stored in the accumulated snowpack was released within the first 30% of meltwater. Mortality of fish (Leivestad and Muniz 1976) and invertebrates (Hall et al. 1980) was observed in streams with an episodic input of H^+ to pH 4.0. During high water in spring this sudden release of H^+ during the first phase of snowmelt could significantly affect sensitive biotic communities and nutrient flux.

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Age at First Maturity and the Early Expression of Oocyte Recruitment Processes in Two Forms of Atlantic Salmon (*Salmo salar*) and Their Hybrids[1]

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Sutterlin, A. M., and D. MacLean. 1984. Age at first maturity and the early expression of oocyte recruitment processes in two forms of Atlantic salmon (*Salmo salar*) and their hybrids. Can. J. Fish. Aquat. Sci. 41: 1139–1149.

The two pure lines and the reciprocal hybrids between an early maturing dwarf form of landlocked Atlantic salmon (*Salmo salar*) and a later maturing anadromous form were reared in captivity for a minimum period of 2.5 yr. Despite similar growth rates, 90% of female parr of the dwarf landlocked strain matured at age 2+ yr (fork length 15 cm), while no females of the anadromous form matured at this time. The weight of the ovary differed in the two pure forms at age 0+ and the numbers, size, and stages of previtellogenic oocytes also differed at age 1+. Ovarian patterns of development and the time of onset of sexual maturation in the hybrid forms appeared intermediate to that of the parental forms. The implications of genetically controlled factors influencing rates of sexual maturation, growth, smoltification, and subsequent fecundity are discussed.

Des spécimens des deux lignées pures et les hybrides obtenus d'un croisement réciproque entre une forme naine précoce du saumon de l'Atlantique (*Salmo salar*) confiné aux eaux intérieures et une forme anadrome à maturité tardive ont été elevés en captivité pour une période d'au moins 2,5 ans. Malgré des taux de croissance semblables, 90 % des tacons femelles de la lignée naine de l'intérieur a atteint la maturité à l'âge de 2+ ans (longueur à la fourche : 15 cm) tandis qu'aucune femelle de la forme anadrome n'était mature à ce moment. Le poids de l'ovaire était différent chez les deux lignées pures à 0+ an; il en était de même pour le nombre, la taille et les stades d'ovocytes prévitellogènes à 1+ an. Les régimes de développement des ovaires et le début de la maturation sexuelle chez les formes hybrides semblaient intermédiaires à ceux des formes parentales. L'ouvrage traite de la portée des facteurs génétiquement contrôlés influençant les taux de maturation sexuelle, de croissance, de smoltification et de la fécondité ultérieure.

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Ovarian development in Atlantic salmon (*Salmo salar*) can be classified as group-synchronous in that distinct cohorts of elements (oogonia, resting oocytes, and vitellogenic follicles) can be observed prior to ovulation (Wallace and Selman 1981; van den Hurk and Peute 1979; Thurow 1966). If the age and size of maturing salmon differ among stocks and are under genetic control, then it may be possible to detect differences in the number of ovarian elements and their patterns of recruitment in juvenile fish from different races. The expression of genes in early life could be a prerequisite in arriving at the required fecundity at the appropriate time.

By examining the early reproductive characteristics of two diverse races of Atlantic salmon and their hybrids, this study was undertaken to reveal (1) the time at which these genetic differences are first expressed during ovarian development and (2) the parental influence controlling the inheritance of such traits.

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Materials and Methods

Characteristics of the Salmon Races

The anadromous salmon used in this study were obtained as eggs from the Exploits River stock, Newfoundland. Wild fish smoltify predominantly at age 4, spend one winter at sea, and return to spawn as 50-cm grilse the following summer (Fig. 1D). Approximately 10% of the fish survive to spawn a second time the following year.

A dwarf landlocked population (Five Mile Pond East, Avalon Peninsula, Nfld.) of salmon was selected as an extreme representative of salmon maturing at a small size. Wild fish seldom exceed 15 cm in length, and aging by scale analyses indicates that such females first spawn at age 3+ at a length of 12 cm (Fig. 1A). This dwarf form has been routinely cultured in our laboratory for the last 6 yr using a natural temperature cycle or using warmer water during the winter. Under natural conditions approximately 6% of females mature at age 1+ (length = 12–14 cm) and 90% at age 2+ (length = 12–18 cm) (Fig. 1B). If eggs are incubated at 8°C and the fish subsequently maintained in heated water (15°C) during the second winter,

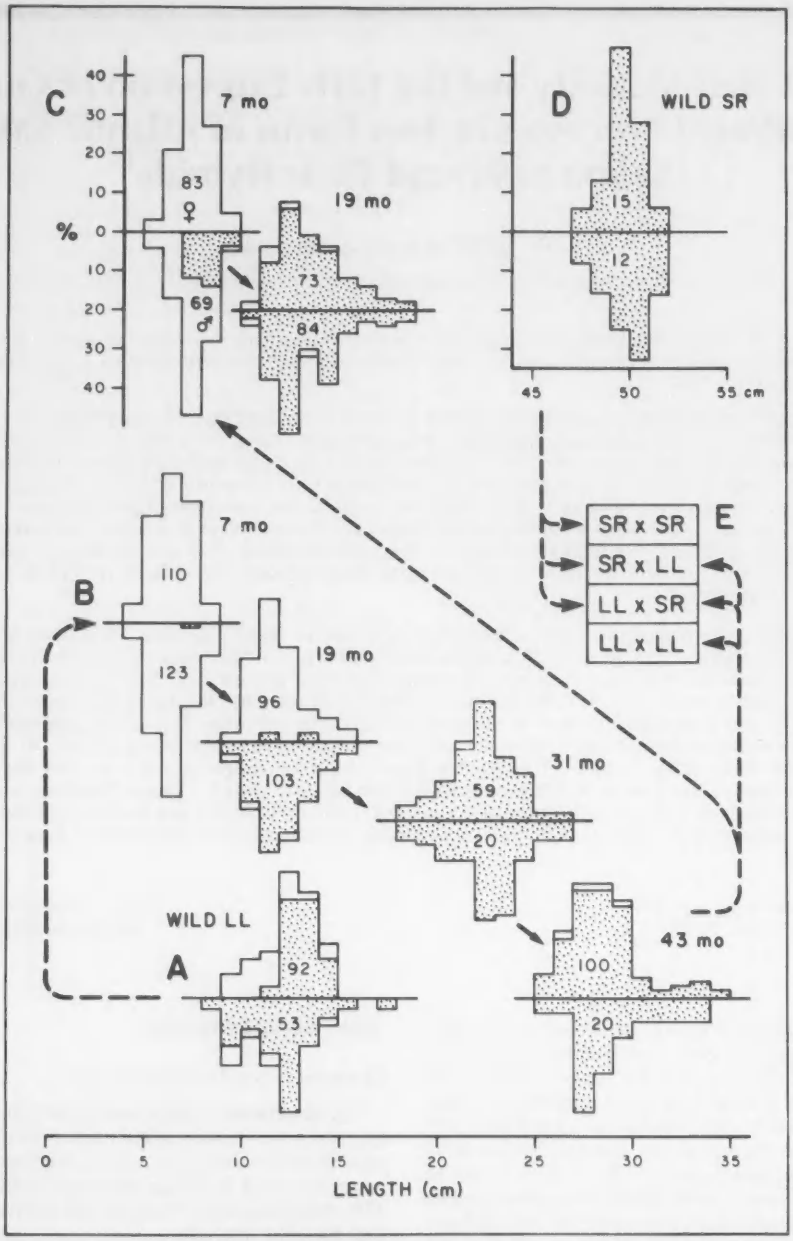

FIG. 1. Parental stock history, size structure, and breeding scheme. A, donor wild LL stock captured at Five Mile Pond East, Nfld.; B, F_1 generation cultured from gametes from A at ambient temperatures; C, F_2, LL × LL accelerated using 8°C water for egg incubation and 15°C water during summer and second winter; D, donor wild SR stock captured in Exploits River, Nfld.; E, diallel crossing scheme using pooled gametes from B and D. Shaded portions of histograms represent mature or maturing fish with females above and males below axis. The age and numbers of fish examined are indicated. LL = dwarf, landlocked salmon; SR = anadromous salmon. Solid lines connect the same group of fish between growth intervals, and dotted lines indicated the flow of gametes. Except for D, the length scale on the bottom is common to all histograms.

90% of females will mature at age 1+ yr (Fig. 1C). Similarly, a larger proportion (30%) of males can be induced to mature 1 yr earlier when accelerated as above (Fig. 1B and 1C). Postspawning mortality is greater in males than females, and most females have spawned three to four consecutive times while kept in captivity.

Hybrid Crosses and Culture Conditions

In early November, the eggs from 10 anadromous females that had returned from sea were pooled as was milt from 10 males. Similarly, the eggs and milt from 40 females and 20 male landlocked salmon were pooled. These landlocked parents were derived from gametes taken from wild fish 4 yr earlier (Fig. 1A and 1B). A full diallel cross, using pooled gametes, was made resulting in triplicate groups of each of the two hybrid forms and the two pure lines. After hatching, the alevins were reared in 1-m^2 fiberglass tanks for 2.5 yr under natural temperature and photoperiod regimes (minimum winter temperature 1.0°C; maximum summer temperature 17°C). The fish were fed to satiation three times a day on homemade moist pellets. Similar rearing densities were maintained for the different genetic groups. To determine growth rates, the weights and lengths of 50 fish from each of the replicate tanks were measured each month.

The gonadsomatic index (GSI = gonad wt × body wt^{-1} × 10^{-2}) and incidence of sexual maturation among all groups were determined each fall for three successive years. All maturing males were fin clipped to allow for subsequent identification. Throughout this paper the hybrid cross LL × SR represents progeny from dwarf landlocked females bred to Exploits River sea-run males. Time of hatching (April 1) has been designated as age 0 throughout this paper.

Histological Procedures

To determine the degree of sexual maturity, ovaries from fish in each group were collected periodically, examined with a binocular microscope, weighed, and preserved in Bouin's fixative. Each ovary was cleared, embedded in paraffin, sectioned transversely (7 μm), and stained with hematoxylin and counterstained with eosin.

Both ovaries taken from six fish from each of the four genetic groups were examined, and approximately 30 serial sections, taken at three different transects extending the length of the ovary, were selected for analysis. These sections were projected on paper, and the outline of 100 oocytes of each developmental stage was traced. The developmental stage of each oocyte was noted according to the following classification described for rainbow trout (*Salmo gairdneri*) by van den Hurk and Peute (1979):

Stage	Oocyte diameter (mm)
1. Nucleus with one large nucleolus	0.01–0.02
2. Numerous small nucleoli in the periphery of the nucleus; dark-staining Balbiani bodies around nucleus	0.02–0.10
3. Balbiani bodies dispersed as "yolk" nuclei to the periphery of the ooplasm. Cytoplasm loses basophilic character; theca and granulosa layer apparent	0.10–0.30
4. Chromophobic "yolk vesicles" formed in cytoplasm	0.4–1.1
5. Eosinophilic yolk granules formed in periphery of ooplasm	0.5–1.5
6. Yolk granules aggregate and migrate to center of ovum	1.5–3.0

The relative abundance of each of the oocyte stages was estimated by counting only those oocytes of each stage in which the nucleus was present. As no corrections were made to account for differences in nuclear diameter, the abundance of later stage oocytes are overestimates.

A Zeiss magnetically operated planimeter (MOP) was used to determine the circumference of oocytes. The oocyte was assumed to be spherical, and calculations of oocyte diameter (D), based on MOP-determined circumference (C), was arrived at by $D = C\pi^{-1}$. Only those oocytes that were sectioned through the nucleus were used to determine oocyte diameter. From the analysis of serial sections, the nucleus was found to be centrally located, and the ratio of nuclear to oocyte volume for oocyte stages 2, 3, 4, and 5 was 0.13, 0.079, 0.028, and 0.008, respectively. By restricting the MOP analysis to oocytes in which the nucleus was present, an average error in underestimating true diameter of oocyte stages 2, 3, 4, and 5 was 10, 6.5, 3.2, and 1.2%, respectively. This error was considered acceptable in arriving at approximately oocyte diameter.

Results

External Appearance, Growth, and Smoltification

Based on general external appearance, it was impossible to distinguish between the four groups of fish prior to the onset of sexual maturity in females. Preliminary results indicate that certain meristic characters were different between the SR × SR and LL × LL groups, but these results will not be considered further in this paper.

Both the LL × LL and LL × SR fry were smaller than SR × SR and SR × LL fry. This difference persisted for 3 mo following swim-up and is attributed to the small eggs produced by LL dams (Fig. 4). However, by age 5 mo (September 1), the differences in the size of parr were no longer apparent. No differences in weight, length, or condition factors were apparent either between replicates of the same group or between groups from age 5–17 mo (single-factor ANOVA; $P > 0.05$).

At age 16.5 mo, the incidence of male precocity being high for all four groups, there was no difference in the size of males between the four groups (Fig. 2). By ge 27 mo (July), the males in each group were smaller than the females in the same group, which perhaps indicates that the growth in these males was retarded following maturation the previous fall. Due to the higher mortality rate in males in all groups during the previous winter, females were 10–20% more prevalent than males in all groups by the following spring.

A degree of bimodality had developed in the length–frequency distributions of female SR × LL and SR × SR parr by early November (age 19 mo) that persisted throughout the winter. The upper mode (>15 cm), at least in the SR × SR group, is presumed to have given rise to the 60% of females that smoltified in May and were placed in seawater in early June (Fig. 2). Only 8% of SR × SR males were judged to be smolts at this time and they were also placed in seawater. Both male and female SR × SR smolts exhibited a growth rate during the

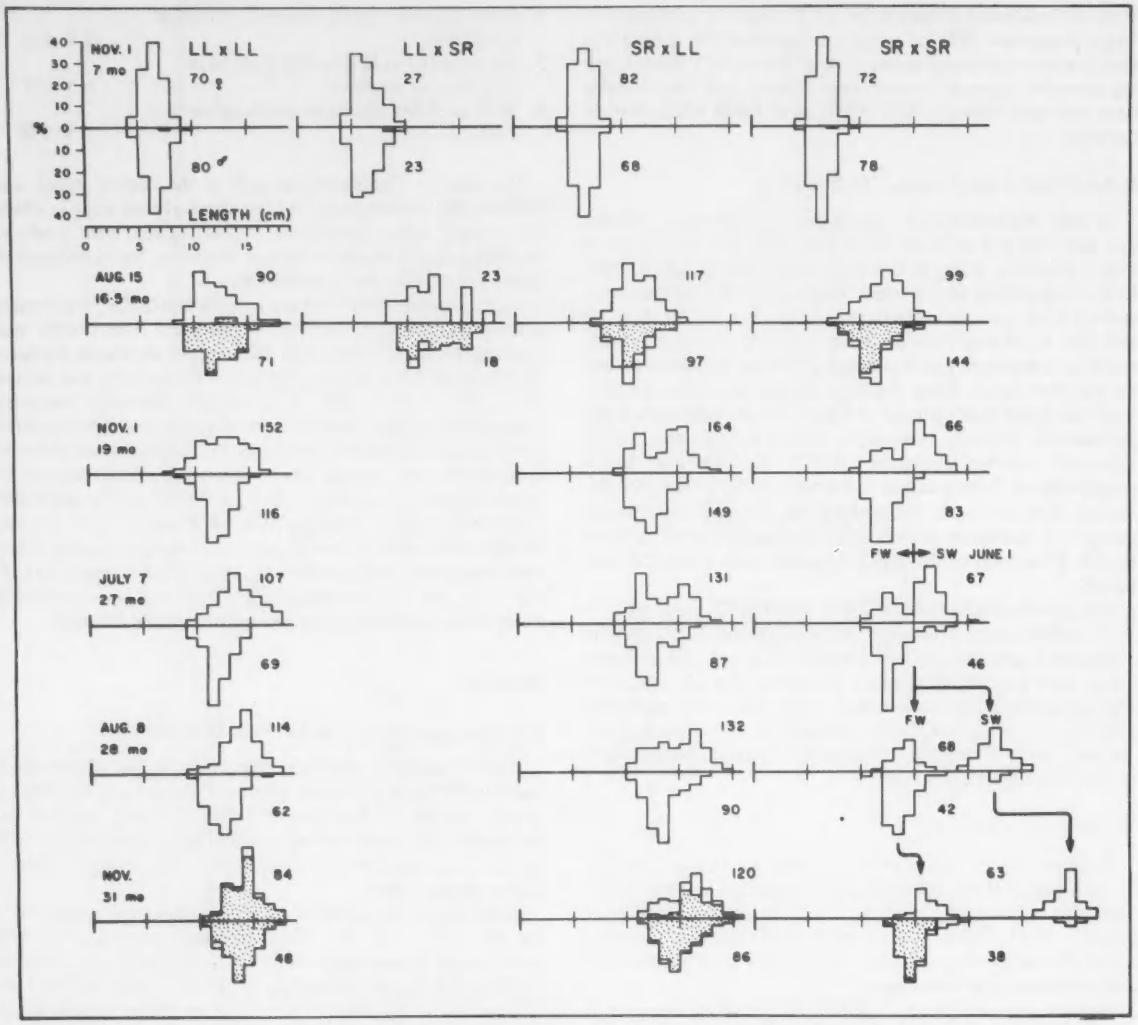

FIG. 2. Size structure and incidence of sexual maturity in the four genetic groups. Equal numbers of fish from each replicate (see Fig. 3) were combined to produce each histogram. August and November histograms were obtained from sacrificed or spawned fish; the remaining histograms were constructed by sampling live fish with adjustments being made for known mortalities and sex ratios determined for fin clipped males. Shaded portions of histograms represent mature or maturing fish with females above, and males below. The sampling date, age, and number of fish examined are indicated. The scale for length is the same for all histograms. SW = seawater; FW = freshwater.

summer in seawater that far exceeded their SR × SR counterparts in freshwater (Fig. 2).

Few LL × LL or SR × LL "smolts" (15–18 cm length), although silvery in color, would tolerate a direct transfer to seawater; their subsequent growth rate during the summer in seawater was less than half that of the SR × SR smolts (not shown in Fig. 2). The LL × LL "smolts" did not exhibit the reduced condition factor that was apparent in the SR × SR smolts.

Sexual Maturity and Fecundity

Less than 3% of males from any of the groups were mature at age 7 mo; at age 16.5 mo, between 50 and 100% of males from the different groups were maturing (Fig. 2 and 3). The incidence of maturity in LL × LL males was significantly higher ($P > 0.05$) than in SR × SR males at 16.5 mo, and the SR × LL and LL × SR hybrids appeared intermediate (Fig. 3).

At age 31 mo, most males from all groups again matured as 2+ yr parr. The reduced numbers of maturing SR × SR male parr are explained by the fact that 15% of the males had smoltified the previous spring and as a result did not mature as postsmolts regardless of whether they were subsequently held in fresh or salt water (Fig. 2 and 3). Among LL × LL and SR × LL males there was no relationship apparent between fish size and the incidence of maturity of age 16 and 31 mo (Fig. 2). Unfortunately, the LL × SR cross perished due to a plumbing failure, and the incidence of maturity age 31 mo could not be determined.

All females from all groups were immature at age 7 mo, and

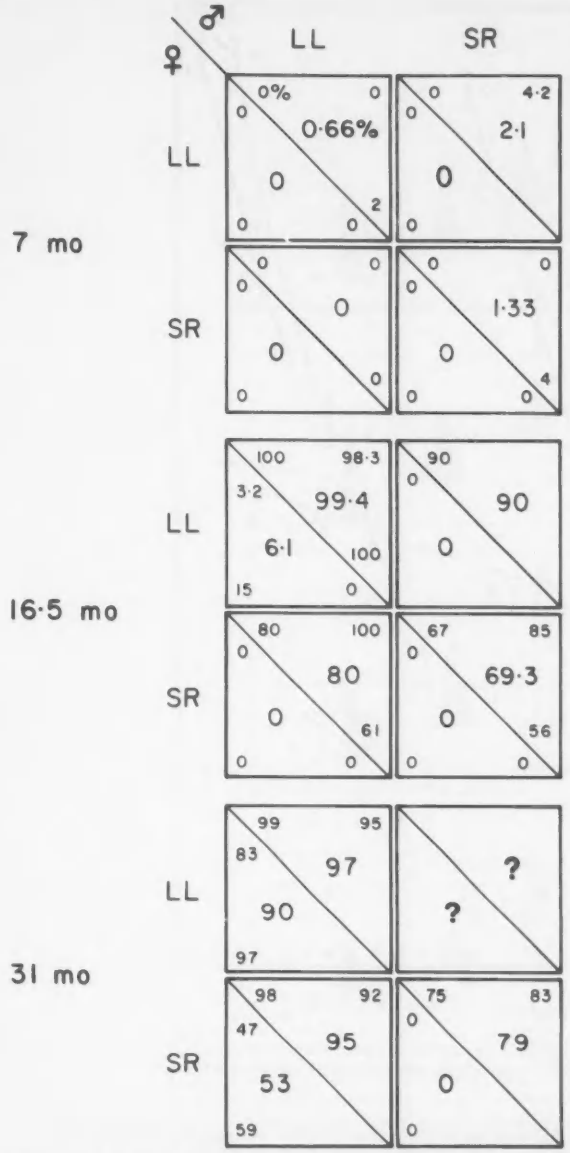

FIG. 3. Percentage of males and females in each group maturing during their first, second, or third summer. Males are represented in a triangle diagonally above the triangle for females. The mean of each replicate is shown as a percentage in the corner of each triangle, and the overall mean of all replicates is shown in the center of the triangle. Total number of fish sampled is indicated in Fig. 2.

at 16 mo only 24 of 270 (6%) females, belonging to the LL × LL groups, were maturing (Fig. 2 and 3). These fish were stripped of eggs 2.5 mo later and yielded an average of 130 eggs per fish (Fig. 4). In groups of LL × LL that were reared prior to this study under similar conditions, over 85% of females matured at age 31 mo and again at age 43 and 55 mo producing 144, 215, and 600 eggs per fish, respectively (Fig. 4). Wild anadromous Exploits River females spawn predominantly at age 43 mo and produce 2000 eggs per female (Fig. 4). At ge 31 mo, 90% of LL

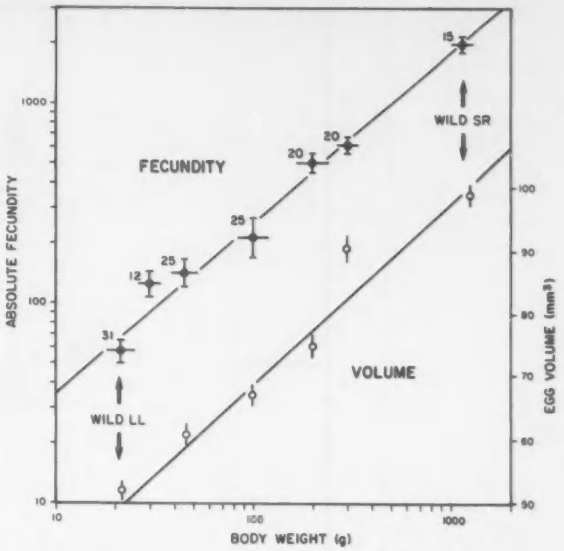

FIG. 4. Body size, fecundity (●), and egg volume (○) of wild and cultured salmon. The extreme points represent the wild landlocked and anadromous salmon, and the intermediate points were derived from cultured landlocked salmon of age 1–5 yr. The number of fish sampled, the mean, and 95% confidence limits are shown. Fitted by eye, $F = 5W^{0.5}$ and $V = 12.5 \ln W + 11.4$.

× LL females matured, and no female SR × SR matured as parr or postsmolts. The SR × LL hybrids appeared intermediate in that 53% of females matured (Fig. 2 and 3).

Female Gonadosomatic Index

The GSI of all groups of female salmon remained below 1.0 until 5–6 mo prior to spawning, and then rapidly increased to levels exceeding 10% (Fig. 5). At age 5 mo, differences in GSI among the genetic groups could be detected in that SR × SR and SR × LL females had ovaries nearly twice as large as ovaries from LL × LL and LL × SR groups (Fig. 5). The following year, the eggs from SR × SR and LL × LL groups were incubated in heated water, and by midsummer again the ovaries of SR × SR females were twice as large as those of nonmaturing LL × LL females (not shown in Fig. 5).

At age 16.5 mo (August), differences in GSI among nonmaturing females in the four groups were no longer apparent (Fig. 5). At this time, a small percentage of maturing LL × LL were detected in that their GSI ranged between 1.5 and 2. These fish probably represent a portion of the 6% maturing females shown in Fig. 2 and 3 that ovulated that fall. At age 25 mo (April), the GSI in LL × LL females, destined to mature during the summer, increased to 0.91, which was significantly higher than in SR × SR or SR × LL females. Somewhat later, between April (25 mo) and August (29 mo), a departure in the value of the GSI occurred between maturing and nonmaturing SR × LL females (Fig. 5). The increase in GSI of maturing SR × LL females continued to lag behind that of LL × LL females, and the spawning time of SR × LL females was delayed 2 wk (Fig. 5). At age 29 and 31.5 mo, there was no difference in the GSI of nonmaturing SR × LL and SR × SR females (Fig. 5). The GSI of wild Exploits River female salmon captured in the river as

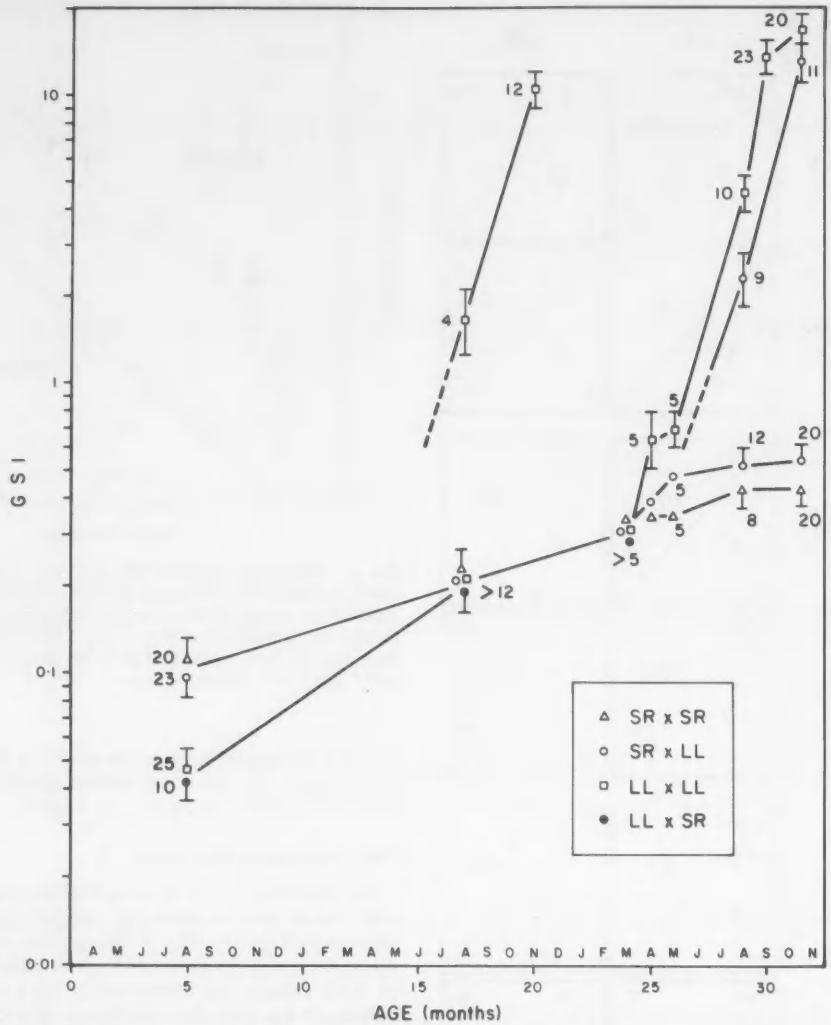

FIG. 5. Changes in gonadosomatic index of maturing and nonmaturing groups of salmon. Broken lines indicate indeterminate projections. The number of fish examined, the mean, and 95% confidence limits are shown.

returning grilse was 1.2% in early June and 21% at spawning 5 mo later.

Oocytes in Fresh Ovaries

While examining the different genetic groups at 16.5 mo (August) to determine onset of sexual maturity, it became apparent using a binocular dissecting microscope that the granular nature of the ovaries of nonmaturing LL × LL and SR × SR females differed. The LL × LL ovaries, although comparable in sizes to the SR × SR ovaries, possessed a number of larger oocytes. Twenty females from each of the above two groups were coded by one investigator, and a second co-worker was asked to separate them based on visual inspection of the ovaries. Only 2 of 40 fish (5%) were categorized incorrectly. The ovaries of LL × SR females also had larger oocytes than SR × LL females, but the error in separating LL × SR from SR × SR was somewhat greater (15%). Attempts to distinguish LL × LL from LL × SR ovaries or SR × SR from SR × LL ovaries were unsuccessful.

The fresh ovaries of 20 females from each of the four groups were again viewed through a binocular dissecting microscope when the fish were age 23.5 mo (March). Oocytes greater than 0.5 mm in diameter were present in all LL × LL and LL × SR females; no oocytes greater than 0.5 mm were present in either SR × SR or SR × LL females. Females from all groups were beginning to become silvery at this time, and it was impossible to distinguish among the four forms of salmon based on external appearance.

At the end of April (25 mo), the ovaries from the 20 LL × LL females could be distinguished from the ovaries of 20 SR × SR and SR × LL females without the aid of the dissecting microscope. The largest oocytes in LL × LL ovaries were three times the size of the oocytes in the other two groups.

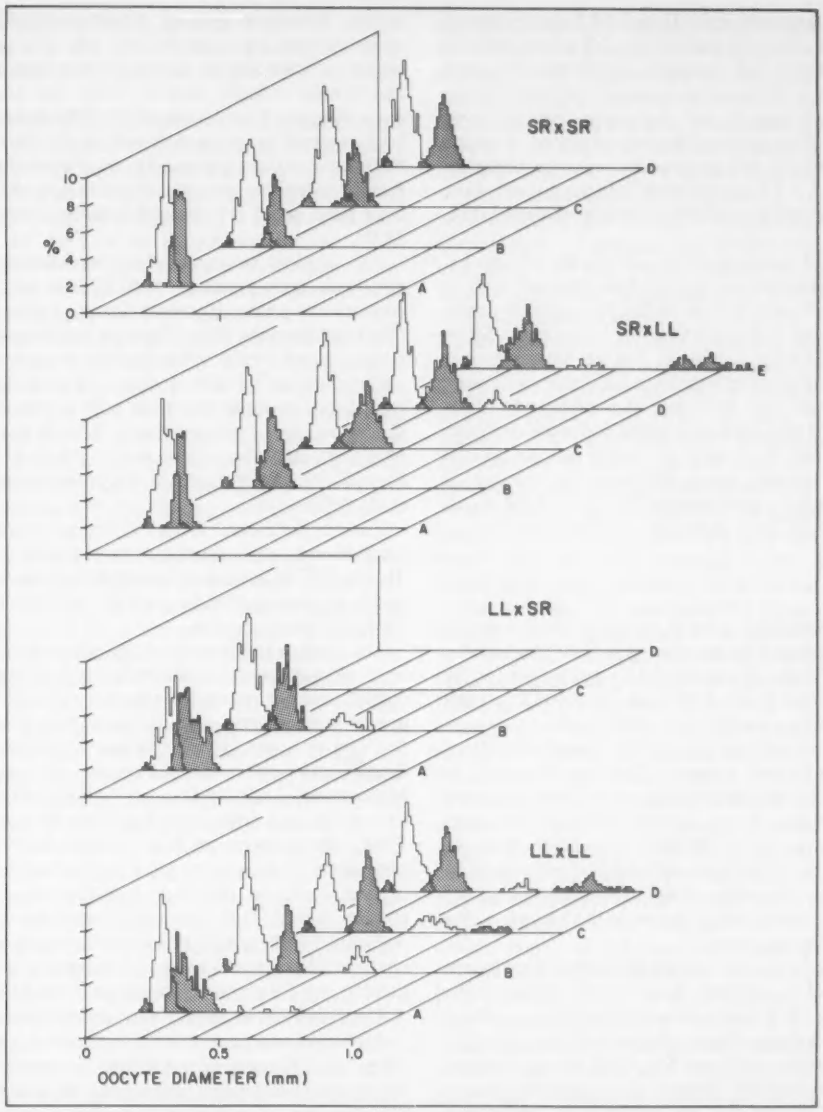

FIG. 6. Oocyte recruitment patterns in the four groups of Atlantic salmon. A, August 15, age 16.5 mo; B, March 15, 23.5 mo; C, April 28, 25.0 mo; D, June 1, 26.0 mo; E, June 15, 26.5 mo. Each series of histograms represents the mean oocytes size and their relative abundance in six ovaries from six different fish. For SR × LL, series D and E, only ovaries from maturing fish are represented. Histograms showing stage 1, 3, and 5 oocytes are stippled.

By June 1 (26 mo), the ovaries from 20 SR × LL females were variable in oocyte sizes and intermediate in appearance between SR × SR and LL × LL ovaries.

Histology of Ovaries

Although 5-mo-old SR × SR and SR × LL females had larger ovaries than the LL × LL and LL × SR (Fig. 5), there was no difference in either the relative number or size of stage 1 and 2 oocytes. Stage 3 oocytes were absent in 5-mo-old females from all groups.

Among the 16.5-mo-old SR × SR and SR × LL ovaries, there was no difference in relative number or size of stage 1, 2, or 3 oocytes (Fig. 6). Stage 4 oocytes were absent in both these groups. Four of the six LL × LL ovaries sectioned contained large (0.31–0.60 mm diameter) stage 4 oocytes, and all six ovaries contained greater numbers of large (>0.25 mm diameter) stage 3 oocytes than ovaries of either SR × SR or SR × LL females (Fig. 6). Ovaries of LL × SR females contained no stage 4 oocytes, but large (>0.2 mm diameter) stage 3 oocytes were abundant in the ovaries of all six fish (Fig. 6). Peripheral yolk granules characteristic of stage 5 were absent in all ovaries examined.

The ovaries of two maturing 16.5-mo LL × LL females that

had elevated GSI contained some large (>1.5 mm diameter) stage 5 and 6 oocytes that had reached the yolk nuclei and yolk coalescent stage. These fish probably represented the small proportion of LL × LL females that ovulated 3 mo later (FIg. 2, 3, and 5). In late April (age 25 mo), oocytes in ovaries of three of the six LL × LL females examined had advanced to stage 5 (Fig. 6), and all ovaries in this group contained stage 4 oocytes. The SR × SR and SR × LL ovaries were indistinguishable from each other in that the oocytes had not advanced past stage 3 (Fig. 6).

At the beginning of June (age 6 mo), all ovaries from six LL × LL females contained large stage 5 oocyte. Stage 3 in SR × SR ovaries exhibited some growth during the previous month but none had advanced to stage 4. Oocytes in two of six SR × LL ovaries contained stage 4 oocytes, and the remaining four ovaries were indistinguishable from SR × SR ovaries with stage 3 oocytes. In mid-June (age 26.5 mo), six ovaries of 14 SR × LL females examined appeared more developed when viewed in a dissecting scope and these were sectioned. All six ovaries contained stage 5 oocytes, suggesting that this fraction of maturing fish represents a subsample of the 53% of SR × LL females that ovulated 4.5 mo later (Fig. 2, 3, and 5).

Discussion

Dwarf forms of landlocked salmon, in which females mature at a small size, have been reported to exist in Newfoundland by Barbour et al. (1979) and Wiseman (1973) and in Norway by Dahl (1928). The extent to which this stunting is due to genetic or environmental factors has not been established.

The island of Newfoundland possesses thousands of isolated populations of landlocked salmon. They are believed to have originated from anadromous ancestors that reinvaded freshwater in postglacial times. Isostatic rebound of coastal regions limited the exchange of their genes with those of anadromous forms and presumably allowed the freshwater type to evolve. Lack of competition from other more temperate freshwater species is also a likely factor in the success of the landlocked salmon on the island.

Considerable diversity exists among landlocked populations in Newfoundland. The extreme dwarf forms appear to be restricted to small ponds in barren areas at high elevation. These ponds are fed by drainage from sphagnum bogs; pH, light penetration, and productivity are low, and forage fish are lacking. At the other extreme, some of the larger lake systems contain landlocked salmon that are considerably larger than anadromous grilse.

A further complication exists in that there are several watersheds on the island that are known to contain both an anadromous and a "resident" form of salmon. In the resident form, maturing males and females can be found that are intermediate in size between smolt and grilse. The origin of these sympatric groups and the extent to which they are reproductively isolated is presently unknown (Payne 1974).

The dwarf landlocked population of salmon selected for this study has been reared in captivity for over three generations, and the reproductive characteristics of females appear stable and different from those of all anadromous stocks that have been cultured in hatcheries in Canada, the United Kingdom, and Scandinavia.

The high incidence of sexual maturity among age 1+ females reared in heated water and 2+ LL females cultured at ambient temperatures is exceedingly rare in anadromous salmon. Because of the dark coloration and plump bodies, these maturing parr are quite distinct, and it is unlikely that they would go unnoticed in hatcheries or research stations rearing anadromous Atlantic salmon. Also, the attainment of 90% maturity at age 2+ by cultured LL × LL female salmon has not been reported in cultured or wild anadromous salmon parr in freshwater, nor does it usually occur in anadromous postsmolt females inhabiting seawater. Some exceptions to this, however, have been noted (Power and Shooner 1966; Sutterlin et al. 1978).

The ambient temperature regime used in our studies has employed approximately 3000°C-days per year, which is conducive to producing predominantly 2-yr anadromous smolts (Goff and Forsyth 1979). The high incidence of male precocity in age 1+ and 2+ SR × SR Exploits River parr obtained in this study is typical of that in many Newfoundland anadromous populations in which few male parr survive to smoltify, most smolts consist of predominantly 3- to 4-yr-old females, and returning adults also consist mostly of female grilse (Davis and Farwell 1975; Chadwick et al. 1978; Moores et al. 1978; Dalley et al. 1983).

The environmental factors affecting growth, maturity, and smoltification of precocious male parr have been examined by Thorpe (1975), Eriksson et al. (1979), Saunders et al. (1982), and Lundqvist and Fridberg (1982) and will not be considered further in this discussion.

The relative importance of age and size in determining the onset of maturation in salmonids has been considered by Alm (1959), and our results with the LL × LL (wild and cultured) appear to be in agreement. Between diverse stocks, it is likely that age, size, and growth rate have a permissive rather than a deterministic effect on maturation (Eriksson et al. 1979; McKenzie et al. 1983). Because the presmolt growth rate of the LL form did not differ from that of the SR form during the first 17 mo, descriptions such as "dwarf" or "stunted" may be misnomers, at least in the physiological sense. The occurrence of such forms in nature is probably better explained by a combination of (1) the reduced time or size necessary to reach maturity, (2) their high incidence of repeat spawning and the continual allocation of energy to gonadal as opposed to somatic growth, and (3) perhaps limitations in food resources.

The difference in age at first maturity in both LL × LL males and females, when reared under different thermal regimes (Fig. 1B and 1C), illustrates the difficulty in using such discontinuous or threshold-dependent characters in quantitative genetics. However, an examination of oocyte recruitment patterns in these different forms of salmon (Fig. 6) indicates that the mode of inheritance of such "quasi-continuous variations" is likely to be similar to that of a continuously varying character (Falconer 1960). Falconer (1960) also pointed out the importance in selection of being able to manipulate only a desired portion of a population across such a threshold.

The larger size of ovaries of 5-mo-old SR × SR and SR × LL crosses may be related to the fact that these fish are destined to mature at a later time and larger sizes than the LL × LL and LL × SR fish. Since neither the size nor relative abundance of oocytes among the four groups differed at this time, the larger ovaries of 5-mo-old offspring derived from the SR dams presumably contain twice as many stage 1 and 2 oocytes. The absolute fecundity of wild LL × LL at first spawning is about 50 eggs. In contrast, wild 3-yr-old SR × SR smolts are destined to produce about 2000 eggs at age 4, or had they smoltified at age 2, they would likely have produced approximately the same

number of eggs at age 3. The differences in ovarian weight between the groups at age 5 mo could represent the early expression of a maternally inherited approach to "family planning."

Although the female GSI of all groups was identical at age 16.5 and 23.5 mo (Fig. 5), the relative abundance and size of the oocytes among the groups were quite different (Fig. 6). It would appear that from the time of sex differentiation to the time of exogenous vitellogenesis, ovarian growth is more rapid than somatic growth, the rates of oocyte recruitment can differ widely among diverse races of salmon, and a critical developmental threshold must be attained by a certain date to permit the oocyte to enter the final vitellogenic phase.

Although the data for the LL × SR hybrid are incomplete, the four patterns of ovarian development in Fig. 6 appear to represent a continuum in which the rate of recruitment is proceeding most rapidly in the LL × LL ovaries with decreasing rates in LL × SR and SR × LL ovaries and at a very low rate in SR × SR ovaries. Based on the presence of stage 4 oocytes in LL × SR ovaries in March (age 15 mo), had these fish lived, we would have anticipated a high incidence of maturing females the following summer.

The different rates of oocyte recruitment among the three surviving groups correlate well with the incidence of maturing females among these groups. Both lines of evidence suggest that the age at first maturity in females is under genetic control.

In addition, the intervening process of smoltification in SR forms could complicate any simple comparisons between the characteristics of maturity of the SR and LL forms. Despite several attempts to introduce male or female 26-mo-old, 12- to 18-cm LL × LL "smolts" directly into seawater during the spring, they seldom live longer than 4 d. Despite a silvery appearance, LL × LL "smolts" have a high condition factor and low salinity tolerance perhaps more typical of presmolt parr. We therefore propose, based on (1) the predestination of the LL × LL "smolts" to mature 5 mo after this "pseudo-smoltification" and (2) the advanced ovarian development observed 2 and 14 mo previously, that the earlier "decision" to mature precludes certain physiological changes that normally accompany smoltification in nonmaturing anadromous females. A similar incompatibility between the processes involved in male precocity and smoltification has been proposed in male salmon (Thorpe and Morgan 1980; Thorpe 1982; Saunders et al. 1982). This hypothesis, however, might not be applicable to other forms of female landlocked salmon that mature at a larger size. The retention of such characteristics as body silvering in landlocked forms would appear to be adaptive in their migration from a fluvial to pelagic existence in lakes. Barbour and Garside (1983) noted similar differences between landlocked and anadromous salmon.

Our results suggest that the presence of the "yolk" vesicle stage (stage 4) prior to June is a prerequisite for vitellogenesis and maturation to occur that summer. Stage 4 oocytes were present in the ovaries of LL × LL and LL × SR females as early as the previous March, but did not develop in the SR × LL ovaries until some time in May (Fig. 6).

If the presence of stage 4 oocytes is indicative of spawning 5–14 mo later in Atlantic salmon, the physiological and biochemical factors responsible for the recruitment of oocytes to this stage have not been established. Stage 4 oocytes are usually considered previtellogenic although presence of "yolk" vesicle has, in some cases, been used as evidence in support of the production of endogenous yolk. Wallace and Selman (1981), however, emphasize that such "yolk" vesicles appear to become the cortical alveoli and are subsequently extruded after fertilization and should therefore not be considered true yolk.

Biochemical and histological studies (Idler et al. 1980) on andromous salmon returning from sea in June in preparation for spawning the following October indicate that oocytes of these fish had surpassed stage 4 in development and the oocytes of most fish had advanced to the midprimary yolk stage (two stages more advanced than the yolk vesicle stage, according to the classification of Ishida et al. 1961). These fish had GSI's exceeding 0.30 and plasma vitellogenin above 100 μg/mL. Thurow (1966) and Templeman (1967) had previously provided evidence, based on oocyte diameters of salmon captured at sea in November and April, that differences were occurring within the ovaries of presumptive spawners and nonspawners in advance of the hormonal and biochemical differences noted above by Idler et al. (1981). In November, Thurow (1966) could distinguish between ovaries taken from large and small salmon. The oocytes of small salmon were all below 0.9 mm in diameter, while a proportion of these from large salmon were greater than 1.2 mm in diameter. He suggested that these two groups of fish represented two and three sea-winter fish, respectively, that were destined to spawn 1 and 2 yr later. Histological staging, however, was not conducted by Thurow.

Oocyte stages of development progressing from the yolk vesicle to the oil globule and early primary yolk stage reported by Idler et al. (1981) in prespawning salmon in June have not been completely accounted for in anadromous Atlantic salmon. Ishida et al. (1961) have shown that oocytes in the group-synchronous ovary of the Kokanee salmon (landlocked sockeye, *Oncorhynchus nerka*) had surpassed the yolk vesicle and reached the oil globule stage (stage 4.5) at least 8 mo in advance of spawning. Recent studies of North Sea capelin, *Mallotus villosus* (Forberg 1982), designate the onset of the yolk vesicle stage as being critical in predicting spawning within the year.

In Atlantic salmon, two critical phases of ovarian recruitment may be taking place several months apart. The first might relate to the commitment to mature or not (recruitment to "yolk" vesicle stage), and the second is perhaps fecundity related (number of oocytes ultimately recruited into vitellogenesis). Both processes are likely to be influenced by somatic energy reserves versus expenditures as well as genetic factors. Under conditions of accelerated growth, cultured LL × LL females can be made to mature at a comparable size but 2 yr earlier than their wild counterparts. However, the eggs taken at first spawning from accelerated females over three successive years could never be fertilized. Similarly, eggs produced by the small percentage of 1+ LL × LL mature females reared under ambient conditions were also infertile. The relative fecundity of these fish was higher and the egg volume lower than all groups shown in Fig. 4 that produced viable eggs. It would appear then that some uncoupling of gametic and somatic coordination has occurred during the accelerated rearing regime.

Experiments on sticklebacks (*Gasterosteidae*) by Wallace and Selman (1979) have shown that lower stage previtellogenic follicles ("yolk vesicle" and below) can be advanced to incorporate exogenous yolk when stimulated with human chorionic gonadotropin, regardless of the stage of oocytes in the leading clutch. However, this is not the case in all species. In juvenile male and female rainbow trout, luteinizing hormone–releasing hormone (LH-RH) analogue is not effective by itself in stimulating gonadotrope activity (GtH production) nor the onset of sexual maturity. In male trout, steroid priming of the

pituitary does elevate plasma GtH and advance sexual development; however, such priming of females elevates GtH but does not result in further ovarian development (Crim and Evans 1983). Thus, it is not clear whether the brain is controlling the ovary or vice versa.

Although the level of gene action on the hyptothalamic, pituitary, and ovarian axes has not been established in salmonids, Schreibman and Kallman (1978) and Bao and Kallman (1982) have shown that in the platyfish (*Xiphophorus*), oocyte development through the oil droplet stage (stage 4.5) occurs in the absence of a functional gonadotropic zone. However, further development depends on the expression of a sex-linked gene that controls the time at which gonadotrophs differentiate. These workers suggested that the gene does not act on the hypothalamus inducing LH-RH release, but appears to control the physiological function or fate of LH-RH.

The relative importance of genetic and environmental influences on the age and size at first maturity in female Atlantic salmon has been a source of speculation for many years (see review by Gardner 1976). Although different river stocks exhibit different incidences of maturation when reared under identical conditions (Naevdal 1981), the heritability of maturation rates of females within a stock has not been easily established, nor has the relative contribution of maternal and paternal factors been especially apparent (Piggins 1974). Environmental factors affecting presmolt history and subsequent marine growth rates can substantially modify the age at first maturation of females (Ritter 1975; Thurow 1966; Sutterlin et al. 1981). This source of variation, coupled with the overlap in ages of first maturity present within and between many anadromous stocks, has complicated most attempts at determining the heritability of such traits in Atlantic salmon.

The incidence of male precocity in Atlantic salmon progeny is, to an extent, influenced by the maturational characteristics of the male parent (Thorpe 1975; Glebe et al. 1978; Thorpe et al. 1983). In our experiments, however, the incidence of maturing males in LL × LL and LL × SR groups was greater than in the SR × SR and SR × LL groups (Fig. 3), which indicates the presence of an influence acquired from the dam.

The selection of two diverse forms of salmon for use in our studies has enabled us perhaps to better separate genetic influences from those of the environment. However, due to the large differences in egg volume of the two parental dams (SR:LL = 3:2), we cannot separate maternal genetic from maternal environmental influences. The larger egg size results in larger fry and this difference in size is maintained during the first 4 mo of feeding. A second complicating factor arose from differences in mortality rates between the two hybrid groups. Prehatching mortality in the LL × SR eggs, measured for three successive generations, has been 10 times greater than in the remaining three groups, and might also be related to egg size. The possibility of linkage between mortality and other traits perhaps cannot be ignored (Payne 1974). In addition to the unique nature of the cytoplasm of the fertilized egg (previously discussed), there is evidence from other animals that the action of maternal genes is dominant from the time of fertilization to gastrulation (Davidson 1976); whether or not maternal influences affect growth and subsequent maturation rates remains uncertain.

Considerable effort is now being expended in breeding programs to develop late-maturing lines of Atlantic salmon for use in mariculture. Based on the additive effects noted in the present study, the commercial culture of F_1 hybrids derived from parental stocks with diverse characteristics of maturity is not likely to be beneficial without further selection.

A proposed salmon enhancement program (Pratt 1983) for the Newfoundland and Labrador region contains plans for the removal of barriers to upstream migration and the seeding of headwaters with anadromous fry and adults. In many systems these headwaters contain established populations of "landlocked salmon." As Payne (1974) pointed out, "with the possible occurrence of gene pool absorption and long term introgression," such proposals should be carefully examined.

The extreme genetic differences in reproductive traits in the two forms of salmon used in this study may (Payne 1974) or may not (Ståhl 1981; Ryman 1983) be similarly expressed as heterogeneities in other allele frequencies (enzyme polymorphisms). It is possible that genetic changes resulting in reproductively different phenotypes can occur more rapidly than changes in other perhaps "less adaptive" allele frequencies. Since traits such as age and/or size at first maturity can also affect growth and mortality rates as well as fecundity, the identification of closely linked biochemical markers would be especially useful. Recently, an enzyme polymorphism (erythrocyte peptidase) was found to be sex linked in a urodele amphibian (Cayrol et al. 1983).

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Multivariate Morphometric Variability in Pacific Salmon: Technical Demonstration

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A computer oriented approach to the collection and analysis of morphometric characteristics in juvenile chinook salmon (*Oncorhynchus tshawytscha*) is described. A three-step data collection and storage method is used whereby *X–Y* coordinate data for relevant morphological features on a body form are collected with a digitizing pad and used to calculate morphometric characters. To test this method, I calculated two morphometric data sets, a conventional and a truss network, and compared them by multivariate analysis in a preliminary study of growth and development in one hatchery stock of fish, and in a survey of population differences in three naturally occurring populations of chinook salmon. Technical advantages of using a digitizing pad for collecting morphometric data are demonstrated. Hatchery-reared chinook salmon showed marked changes in body shape during the period of spring smoltification when marked changes in condition factor occurred. Multivariate differences were discerned among the three Oregon coastal stocks. Truss data provided more specific information concerning shape changes in the study of early development and produced greater between-group differences in the geographic survey. The results of these preliminary analyses can be applied to problems of identifying smolt status in hatchery fish and stock origin in mixed-stock fisheries.

On décrit une approche informatisée à la collecte et à l'analyse de données morphométriques de juvéniles de saumon quinnat (*Oncorhynchus tshawytscha*). Les caractéristiques morphométriques sont calculées à l'aide d'une technique de collecte et de mise en mémoire des données en trois étapes qui fait appel à une plaque pour la collecte, sous forme numérique, des données des coordonnées *X–Y* des caractéristiques morphologiques corporelles. Pour vérifier cette méthode, j'ai calculé deux séries de données morphométriques, une série classique et un réseau, et comparé les résultats obtenus avec ceux d'une analyse à variables multiples lors d'une étude préliminaire de la croissance et du développement d'un stock de poissons élevés en pisciculture, et lors d'une enquête portant sur les différences entre trois populations naturelles de saumon quinnat. Les avantages techniques que représente l'utilisation de la plaque de numérisation pour la collecte des données morphométriques apparaissent clairement. Les saumons quinnats d'élevage ont présenté des variations de la forme marquées lors de la smoltification de printemps, au moment des importantes variations du facteur de condition. Des différences de variables multiples ont été notées chez les trois stocks côtiers de l'Orégon. Les données du réseau ont fourni plus d'informations précises sur les variations de la forme lors de l'étude des premiers stades du développement et permis de noter de plus grandes différences intergroupes lors de l'inventaire géographique. Les résultats de ces analyses peuvent servir à déterminer le degré de smoltification des poissons d'élevage et de l'origine des stocks dans les pêcheries à stocks mixtes.

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Genetically distinctive populations within a species are unique biological entities that are commonly referred to as stocks. It is important to identify the geographical ranges and to determine some of the basic genetic characteristics of such units to manage them better in fisheries comprising mixtures of stocks (Ihssen et al. 1981). For Pacific salmon (*Oncorhynchus* spp.), many approaches to stock identification have been investigated, including studies with parasites, blood types, tagged fish, scales, and meristics. Perhaps most promising, however, are the studies of stock structure of aquatic organisms (including Pacific salmon) that have been undertaken by geneticists at the Northwest and Alaska Fisheries Center since 1966 using the technique of protein gel electrophoresis (Utter et al. 1980). Electrophoretic data provide valuable genetic information for the evaluation of intraspecific variability (e.g. Allendorf and Utter 1979; Ryman et al. 1979; Busack and Gall 1980; Grant et al. 1980; Winans 1980a). Still, complementary data from other sources are needed for a comprehensive view of population differentiation (Clayton 1981; Utter 1981). Techniques that can use preserved specimens, unlike electrophoresis, are often useful. For example, multivariate statistical analyses of morphometric characters have been frequently applied to studies of stock differentiation (Copeman 1977; Sharp et al. 1978; Wilk et al. 1980; Riddell and Leggett 1981; Winans 1980b), but to date, no multivariate information regarding either ontogenetic or geographic variability is available for any species of Pacific salmon.

For the past 30 yr, morphometric investigations have been

based almost entirely on a set of measurements such as those described in the seminal work of Hubbs and Lagler (1947). These conventional morphometric measurements are concentrated along the anterior–posterior body axis and in the head and caudal peduncle regions, producing uneven and biased areal coverage of the entire body form. Workers at the University of Michigan have recently promulgated a new set of morphometric fish measurements called the truss network that gives even areal coverage over the entire fish form (Humphries et al. 1981; Strauss and Bookstein 1982). The method produces a more systematic geometric characterization of fish shape and has demonstrated increased resolving power for describing interspecific shape differences. More measurements in general though are required for a truss network analysis. The extra effort to take more measurements can be reduced, if not eliminated, through use of a digitizer and computer.

My objectives were (1) to describe a computerized approach to the collection and analysis of morphometric data using juvenile chinook salmon (*Oncorhynchus tshawytscha*) and (2) to analyze multivariately and compare two morphometric data sets, a conventional and a truss network, in a preliminary study of growth and development in a hatchery stock of fish, and in a survey of population differences in three naturally occurring populations of chinook salmon. These results can be applied as possible solutions to specific problems associated with salmon husbandry and fisheries management.

Materials and Methods

Morphometric measurements were made on specimens by collecting X–Y coordinate data for relevant morphological features, and followed a three-step process as follows.

1. Positioning

Specimens are placed on water-resistant (i.e. plastic impregnated) paper, and body posture and fin positions are teased into a natural position. Positioning of specimens in this fashion is a precise process, as evidence by low measurement error (see Results).

2. Pinning

Morphological features or landmarks that are distinctive and homologous from specimen to specimen are selected around the outline of the fish form. Each landmark is indicated and recorded by making a hole with a dissecting needle in the water-resistant paper alongside its respective location. The 15 landmarks I used are illustrated in Fig. 1. Data such as specimen number, body weight, and color are recorded alongside each specimen and added to the computer file when the landmark holes for that specimen are digitized. A sheet of expanded polystyrene (2 mm thick) placed beneath the water-resistant paper facilitates this step.

3. Digitizing

After the landmark information from a set of specimens has been recorded (pinned), the paper is placed on an X–Y coordinate digitizing pad to establish a reference set of X and Y axes to view interlandmark distances. The X–Y coordinate values (±0.01 mm) for the positions of the landmarks are indicated and recorded on a computer by depressing an attached digitizing stylus into each hole. Landmarks are digitized in the same sequence for each fish. Specimen identifying data are added via a computer terminal/keyboard and also stored with the digitized information. The Euclidean or morphometric distances between pairs of landmarks (Fig. 1) are then calculated by computer (using the Pythagorean theorem).

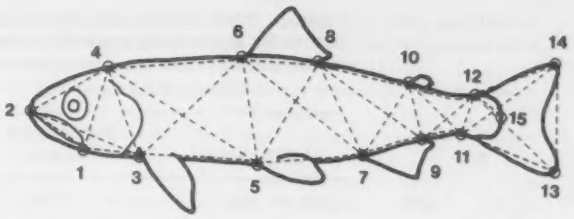

FIG. 1. Locations of 15 landmarks for a truss network data set are illustrated as open circles and morphometric distance measures between circles as broken lines. Landmarks refer to (1) posteriormost point of maxillary, (2) anterior tip of snout at upper jaw, (3) origin of pectoral fin, (4) most posterior aspect of neurocranium, i.e. beginning of scaled nape, (5) origin of pelvic fin, (6) origin of dorsal fin, (7) origin of anal fin, (8) insertion of dorsal fin, (9) insertion of anal fin, (10) origin of adipose fin, (11) anterior attachment of ventral membrane from caudal fin (not least depth of caudal peduncle), (12) anterior attachment of dorsal membrane from caudal fin (see No. 11), (13) most posterior–ventral point of naturally extended caudal fin at tip of second caudal ray, (14) most posterior–dorsal point of naturally extended caudal fin at tip of second caudal ray, and (15) base of middle caudal rays. For landmarks 1 and 3, points are made at their respective positions at the closest point to the body on a line perpendicular to the horizontal axis of the specimen.

With this method I calculated a conventional set of measurements and a truss set of measurements using the 15 landmarks illustrated in Fig. 1. Truss network measurements are a series of measurements calculated between landmarks that form a regular pattern of contiguous quadrilaterals or cells across the body form. Cells and truss characters are referenced according to the scheme of Strauss and Bookstein (1982), e.g. the distance between landmark 1 and 2 is truss character 1–2 in cell 1 (see Table 1). Measurements were made on the left side of each specimen, and all specimens were freshly thawed prior to pinning. Tissues from each specimen were used later for protein gel electrophoresis.

To measure the precision of the digitizing approach to morphometric data collection, I used 10 freshly thawed specimens ranging in size from 8.8 to 13.6 cm and measured each independently five times. Conventional and truss data sets were calculated from the same digitized data for a comparison. The standard deviation of each distance character over the five replications was estimated for each fish; the average standard deviation of a character over the 10 fish was used as an estimate of measurement error.

To learn whether multivariate shape changes could be detected in the early life history of chinook salmon, progeny derived from a fall-run stock of chinook salmon (Green River State Salmon Hatchery, Auburn, WA) were reared and studied at the National Marine Fisheries Service laboratory, Seattle, WA, and at the Garrison Springs State Salmon Hatchery, Fort Steilacoom, WA. Samples of approximately 50 fish were taken monthly from each hatchery after the fish had reached about 5 cm in length and stored frozen until distance measurements could be taken by the described procedures. Body form development was studied exclusive of fin size and shape variation in fish from these hatcheries by analyzing 11 conven-

TABLE 1. Measurement error (mean standard deviation for 10 fish measured five times each) for two digitized morphometric data sets using 10 chinook salmon, 9–14 cm fork length.

Conventional data		Truss data		
Character	Measurement error (mm)	Cell	Character	Measurement error (mm)
Upper jaw length	0.36	1	1–2	0.36
			1–3	0.38
			2–3	0.45
Head depth	0.38		1–4	0.38
Forehead length	0.29		2–4	0.29
		2	3–4	0.45
			3–5	0.61
			4–5	0.46
			3–6	0.40
			4–6	0.64
Body depth at dorsal fin	0.36	3	5–6	0.36
			5–7	0.59
			6–7	0.44
			5–8	0.33
			6–8	0.44
		4	7–8	0.34
			7–9	0.35
			8–9	0.34
			7–10	0.40
			8–10	0.50
		5	9–10	0.29
			9–11	0.42
			10–11	0.39
			9–12	0.33
			10–12	0.38
Depth of caudal peduncle	0.20	6	11–12	0.21
			11–13	0.50
			12–13	0.33
			11–14	0.37
			12–14	0.50
			13–14	1.02
Predorsal length	0.58			
Snout to adipose	0.50			
Fork length	0.31			
Snout to anus	0.44			
Snout to pelvic fin	0.45			
Snout to pectoral fin	0.45			

tional distance characters and 26 truss characters (cells 1–5 and character 11–12). All measurements were calculated from the same digitized data set. Principal component analyses were performed on the total variance–covariance matrix of the morphometric measurements to view changes in character covariability during early growth and shape development (Atchley and Bryant 1975; Green 1976).

The applicability of this multivariate approach to a study of interpopulation differentiation of chinook salmon was evaluated using samples of juvenile fish seined from three Oregon estuarine habitats in August 1981. To detect the maximum amount of multivariate variation, across-group means relative to within-group variation, morphometric differences among the samples were viewed by discriminant function analyses (Atchley and Bryant 1975; Green 1976).

The two multivariate statistical analyses, principal component and discriminant function, summarize the variability and covariability of the original n morphological variables. Both procedures reduce the n-dimensionality of the data to a few principal component or discriminant factors that are linear combinations of the original (= morphometric) data and that represent specific, multivariable complexes of size and shape variability (Atchley and Bryant 1975). Principal component analyses were executed on variance–covariance matrices using a combination of subroutines from the IMSL Library (1977). Multiple discriminant function analyses were performed by the *Statistical Package for the Social Sciences* subprogram DISCRIMINANT, method = direct (Nie et al. 1975). All measurements for both analyses were transformed to common logarithms to reduce the correlation of the measurement means and variances (Sokal and Rohlf 1969). Bivariate confidence ellipses were used in several illustrations to characterize the scatter of points about simple means and were calculated by Program A3.13 in Sokal and Rohlf (1969).

Results

Measurement Error

Measurement error was generally less than 0.5 mm and there was not a significant difference between the results for the two

TABLE 2. Principal component (PC) loadings from analyses of juvenile chinook salmon grown at NMFS, Seattle, WA (SEA), and Garrison Springs Salmon Hatchery, Fort Steilacoom, WA (GAR). Eleven conventional characters and 26 truss characters were analyzed separately for each sample. Sheared principal component II (SPC II) values are adjusted by the sheer algorithm of Humphries et al. (1981).

Conventional data					Truss data					
	SEA		GAR				SEA		GAR	
Character	PC I	SPC II	PC I	SPC II	Cell	Character	PC I	SPC II	PC I	SPC II
Upper jaw length	0.29	0.29	0.29	−0.01	1	1–2	0.18	0.07	0.18	0.06
						1–3	0.20	−0.09	0.21	−0.03
						2–3	0.19	00	0.20	0.02
Head depth	0.28	−0.17	0.26	−0.06		1–4	0.17	0.07	0.16	0.11
Forehead length	0.26	0.07	0.26	0.25		2–4	0.16	0.05	0.16	0.01
					2	3–4	0.19	0.07	0.18	0.16
						3–5	0.20	0.06	0.20	0.01
						4–5	0.21	0.03	0.21	0.06
						3–6	0.20	0.11	0.19	0.14
						4–6	0.21	−0.02	0.21	0.06
Body depth at dorsal fin	0.32	−0.75	0.31	−0.37	3	5–6	0.20	0.15	0.20	0.20
						5–7	0.23	0.10	0.22	−0.06
						6–7	0.21	0.08	0.21	0.05
						5–8	0.20	0.18	0.19	0.17
						6–8	0.18	0.02	0.18	−0.02
					4	7–8	0.22	0.13	0.21	0.07
						7–9	0.18	0.14	0.18	0.11
						8–9	0.21	0.09	0.21	−0.02
						7–10	0.20	0.10	0.20	0.15
						8–10	0.24	0.06	0.25	−0.13
					5	9–10	0.18	0.05	0.18	0.15
						9–11	0.20	−0.86	0.21	−0.80
						10–11	0.18	−0.18	0.18	−0.11
						9–12	0.19	−0.18	0.20	−0.13
						10–12	0.18	−0.16	0.18	−0.20
Depth of caudal peduncle	0.27	−0.34	0.29	−0.77		11–12	0.17	0.07	0.18	0.25
Predorsal length	0.31	0.07	0.30	0.09						
Snout to adipose	0.33	0.17	0.33	0.23						
Fork length	0.31	0.16	0.31	0.22						
Snout to anus	0.33	0.13	0.32	0.21						
Snout to pelvic fin	0.32	0.05	0.32	0.16						
Snout to pectoral fin	0.30	0.36	0.31	0.17						

data sets (Table 1). With the exception of character 13–14, measurement error in the truss data ranged from 0.21 to 0.64 mm (mean = 0.40). The mean measurement error per cell was low in cells 1, 4, 5, and 6 (averaging about 0.37 mm), whereas cells 2 and 3, representing the trunk and midbody cells, respectively, had slightly higher mean values. The measurement of the distance between the dorsal and ventral tips of the caudal fin had the largest measurement error (1.02 mm). For the conventional data set, measurement error ranged from 0.20 to 0.58 mm (mean = 0.39 mm). The smallest measurement errors were recorded for the characters associated with the head (forehead and upper jaw), body depth, and the fork length. Theoretically, measurement errors can radiate from the repeatedly used landmarks throughout a traditional data set much more effectively than in the truss data (Strauss and Bookstein 1982), but no evidence of this phenomenon is indicated in these data: measurement error for truss characters equalled the measurement error for the traditional measurements. Overall, measurement error was small and within a range suitable for morphometric investigations of fish.

Developmental Changes

The study of body shape development was conducted with one stock of salmon raised in two locations: Seattle, WA (SEA), and Garrison Springs State Salmon Hatchery, Fort Steilacoom, WA (GAR). Hatchery water temperatures ranged from 8 to 17°C in the Seattle hatchery and from 10 to 12°C in the Garrison Springs hatchery. Both groups were fed rations of commercial moist-pellet diets. Sampling of fish at GAR was initiated and terminated earlier than SEA because of warmer water temperatures and the need to release fish earlier. It is assumed that the first samples from SEA and GAR represent fish at the same developmental state.

In the two separate analyses of SEA and GAR fish using truss data, approximately 98% of the total variance was explained in each analysis along the first two principal component axes. Principal component I (PC I) was a measure of general size, as indicated by the roughly equal and positively signed coefficients for all the variables on this component (Table 2) and by the relative positions of the samples along the PC I axis (Fig. 2A). An initial analysis showed that PC II contained both size and shape information. Therefore, the second component was adjusted or "sheared" by the algorithm of Humphries et al. (1981) to produce a size-free shape component, sheared PC II (SPC II). In both SEA and GAR analyses, SPC II was mainly a contrast of four measurements in the caudal peduncle and

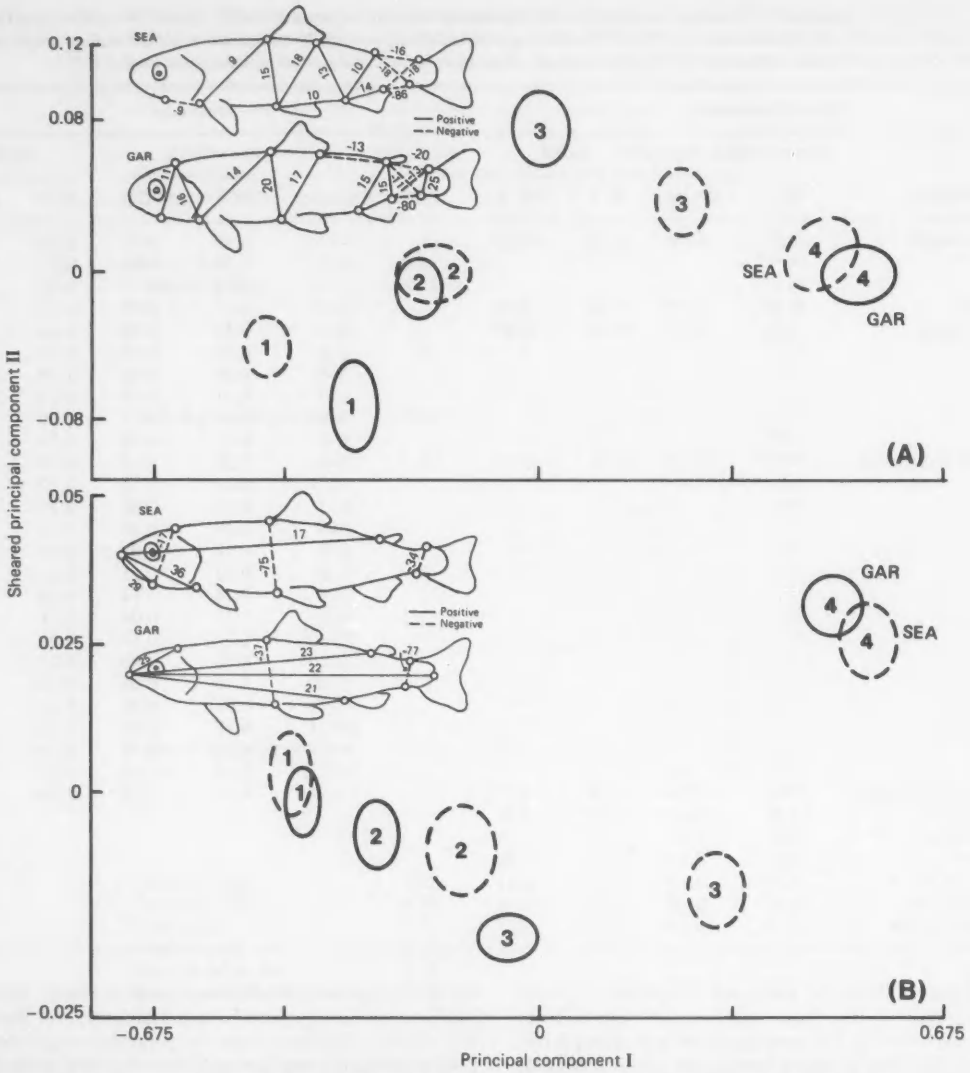

FIG. 2. Ninety-five percent confidence ellipses for bivariate means from analyses of one stock of chinook salmon raised in two locations, NMFS, Seattle, WA (SEA), and Garrison Springs Salmon Hatchery, Fort Steilacoom, WA (GAR). Truss network characters (A) and conventional morphometric characters (B) were measured on each fish and analyzed separately. Insert illustrates important characters that largely account for morphological shape differences on respective sheared principal component II axes. Collection dates in 1982 for SEA samples were (1) 24 May (n = 51), (2) 28 June (n = 49), (3) 28 July (n = 41), and (4) 30 August (n = 44) and for GAR samples were (1) 11 February (n = 49), (2) 2 March (n = 45), (3) 1 April (n = 50), and (4) 18 May (n = 49).

several diagonal measurements in the second, third, and fourth cells, since the coefficients of these measurements were of opposite signs while the other coefficients were relatively small (measurements with relatively large coefficients are illustrated in the insert, Fig. 2A). SPC II was thus an indicator of shape variability associated primarily with the caudal peduncle truss cell. Following a gradual increase in the average SPC II scores for the first three samples, the mean SPC II value in the fourth sample showed a slight decline, particularly in the GAR samples. The correspondence between the results of the independent analyses of SEA- and GAR-reared fish was high: the SPC II variable coefficients from SEA and GAR were correlated (Spearman's rank coefficient, r_s = 0.658, $P <$ 0.001).

In the analyses of the same SEA and GAR specimens using conventional data, approximately 99% of the variance was explained in each analysis along the first two PC axes. PC I was a size factor: all the variables had positive coefficients for this component (Table 2), and the mean fish size increased from left to right along this axis (Fig. 2B). The second principal component was sheared to eliminate size influences. Again, along the SPC II axis, the average value for sample 4 departed from the trend seen in the first three samples (Fig. 2B). The important variables in SPC II involved a contrast between three

TABLE 3. Location and descriptive statistics for three wild-reared samples of chinook salmon in Oregon. Fish were caught within a 5-d period in August 1981. Condition factor = 100·(weight)·(fork length)$^{-3}$.

		No. of fish	Mean		
			Fork length (cm)	Weight (g)	Condition factor
Tillamook Bay	45°33′N, 123°55′W	56	12.11±0.97	22.2±5.6	1.23±0.05
Alsea Bay	44°26′N, 124°02′W	50	11.92±0.88	21.4±4.9	1.24±0.05
Sixes River	42°50′N, 124°30′W	50	9.60±0.62	10.9±2.3	1.22±0.06

depth measurements (head depth, body depth, and caudal peduncle depth) and several length-associated measurements (e.g. fork length, snout to adipose length, etc.; insert, Fig. 2B). Thus, SPC II was an indicator of body slenderness. The patterns of character weightings on SPC II from the analyses of SEA and GAR fish were similar: the rank correlation for SPC II variable coefficients approached the $P = 0.05$ level (Spearman's rank coefficient, $r_s = 0.58$, $0.05 < P < 0.10$).

The early life history of anadromous salmon is marked by a smoltification period during which considerable physiological, biochemical, and behavioral changes occur as the young fish prepare for the transition from a freshwater to seawater habitat. Moreover, during smoltification the fish become more elongate and slender, as indicated by a change in the condition factor (CF) index, where CF = 100·(weight)·(fork length)$^{-3}$ (Hoar 1976; Folmar and Dickhoff 1980; Wedemeyer et al. 1980). A plot of the average condition factor values reveals a pattern similar to those seen in Fig. 2A: the mean condition factor increased in samples 1 through 3 and then decreased in sample 4 in both SEA and GAR samples (Fig. 3). By inference, the changes in SPC II values seen between samples 3 and 4 for both data sets for fish from both hatcheries are indicative of a presumed smolting event.

The expression of morphometric covariability is influenced to some degree by the nature and timing of environmental variation during development. Thus, the concordance of the two results from the multivariate analyses of one genetic stock grown in two separate hatchery environments suggests the presence of a distinct and describable shape change in the early development of chinook salmon. The view of character change is only slightly altered by the geometric nature of the input data set, as the results from the analyses of both truss network and conventional character sets suggest an elongation phenomenon in this phase of development. The conventional morphometric data indicate a change in the body depth/body length relationship, whereas the results of an analysis of the truss data set indicate a specific localized change in the shape of the caudal peduncle (Table 2). Therefore, a multivariate description of morphometric shape changes in early juvenile development appears to be possible with this analytical approach. It should be noted that the greatest change between samples 3 and 4 was observed in the conventional data.

Population Differences

The study of between-stock differences was conducted on 156 fish collected from three Oregon estuaries. Fish were presumably outmigrant smolts (based on location, coloration, time of year, and behavior) of wild stocks. No hatchery fish were present in the estuarine systems at that time (J. Nicholas, Oregon Department of Fish and Wildlife, pers. comm.).

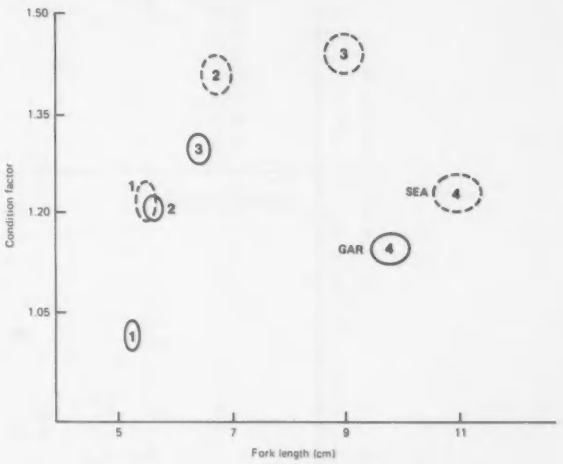

FIG. 3. Ninety-five percent confidence ellipses for bivariate means of condition factor (CF) and fish length for chinook salmon raised in Seattle (SEA) and Garrison Springs (GAR) where CF = 100·(weight)·(fork length)$^{-3}$. Numbers refer to sequential sampling dates given in Fig. 2.

Average fork length per sample varied slightly from 12.1 cm in the Tillamook sample in the north to 9.6 cm in the Sixes River sample 300 km to the south (Table 3). Condition factor did not vary significantly between the three samples (H_0 = no difference, $P = 0.07$; Table 3).

Samples were distinctive along discriminant function (DF) axes I and II. For both data sets, DF I separated fish primarily by size and DF II distinguished the Alsea River sample from the other two samples (Fig. 4). Characters with relatively large coefficients on the DF II vectors were associated with the pelvic and anal fin positions, i.e. characters 4–5(−), 5–6(+), and 6–7(−) in the truss results and snout to anus (−), snout to pelvic (+), and fork length (+) in the conventional data set (Table 4). Although there was little overlap of populations in both analyses, the analysis of the truss characters produced the greatest group separation. For example, the average Euclidean distance between the three sample means was greater in the truss analysis (4.15 versus 3.33).

A classifiction procedure also indicated greater differentiation with the truss data. The classification procedure uses the discriminant function results to identify the likely group membership of each of the 156 fish given only the original measurements for each fish (i.e. it is a "blind" test). The percentage of fish correctly classified to group is an indicator of the discriminatory ability of the discriminant function results. Eighty-six percent of the fish were correctly classified to their

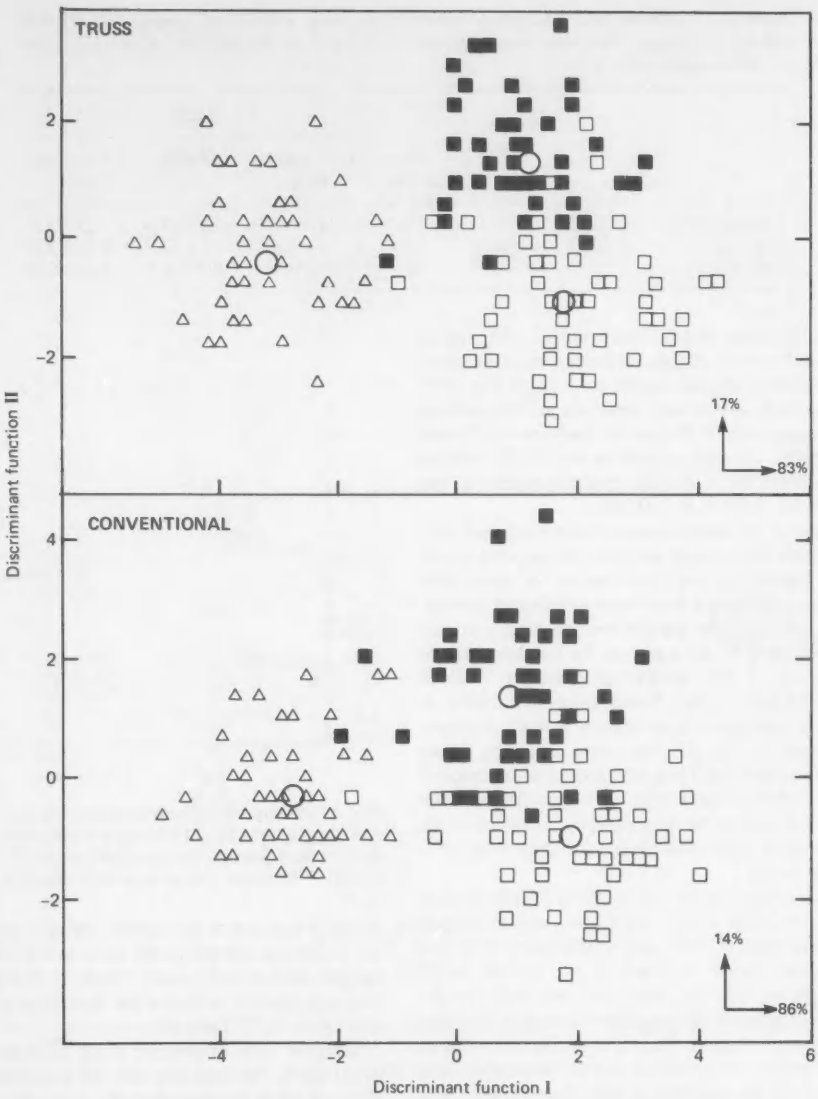

FIG. 4. Scatter plot of discriminant function scores and sample means along the first two axes in two separate analyses of juvenile chinook salmon from Oregon using either truss or conventional data (see Tables 3 and 4). □, Tillamook Bay; ■, Alsea River; △, Sixes River; ○, sample mean.

respective groups using conventional measurements, whereas 90% of the fish were correctly classified using truss data. I conclude that discriminant function analyses can clearly differentiate between individuals of juvenile chinook salmon in different groups separated only by 300 km of coastline, and the choice of data for maximal group discrimination is the truss character network set.

Discussion

The identification of key morphological features around the body outline of juvenile salmon is accomplished with high precision using a three-step digitizing procedure. The observed measurement error over 42 characters was approximately 0.40 mm. For the 26 truss network characters, 90% of them were repeatable within ±0.5 mm, an error level suitable for most ichthyological research. In a recent study of the marine toad *Bufo marinus*, Lee (1982) reported an average measurement error of 0.45 mm (SD = 0.25 mm) for 20 morphometric characters taken with hand-held calipers. In a study of the milkfish *Chanos chanos*, the measurement error associated with hand-held calipers and a measuring board was 0.48 mm (SD = 0.36 mm) for 20 conventional morphometric characters. Given the taxonomic and experimental differences between the reports of Lee (1982), Winans (1980b), and the present work, the digitizing approach is at least as good as, and perhaps better

TABLE 4. Standardized discriminant function (DF) coefficients from analyses of three samples of Oregon chinook salmon using two different morphometric data sets.

Conventional data			Truss data			
Character	DF I	DF II	Cell	Character	DF I	DF II
Upper jaw length	−0.86	−0.28	1	1–2	1.85	1.13
				1–3	2.84	1.31
				2–3	−5.66	−3.28
Head depth	1.29	−0.74		1–4	0.07	0.61
Forehead length	−0.72	1.07		2–4	0.29	−0.74
			2	3–4	−0.23	2.79
				3–5	−2.23	5.74
				4–5	5.87	−11.94
				3–6	2.02	−6.66
				4–6	−3.07	6.93
Body depth at dorsal fin	0.4	−2.20	3	5–6	−1.58	8.90
				5–7	0.29	3.13
				6–7	−3.37	−12.10
				5–8	0.55	−5.42
				6–8	0.74	2.26
			4	7–8	1.58	4.49
				7–9	−0.61	−2.73
				8–9	1.33	7.97
				7–10	0.98	4.90
				8–10	−0.04	−4.36
			5	9–10	−1.04	−3.60
				9–11	0.26	−1.96
				10–11	−0.12	1.53
				9–12	0.12	2.87
				10–12	0.16	−1.22
Depth of caudal peduncle	0.18	−0.86		11–12	0.23	−0.52
Predorsal length	−1.17	−1.90				
Snout to adipose	2.42	−0.76				
Fork length	−0.30	2.34				
Snout to anus	−1.17	−3.55				
Snout to pelvic fin	0.89	3.63				
Snout to pectoral fin	0.09	1.33				
Percentage of overall explained variation	86.40	13.60			82.90	17.10

than, a traditional manual technique for collecting precise morphometric data. In general, as Lee (1982) also reported, some characters may be more precisely measured than others (e.g. characters in cell 6). To the large extent that morphometric data are used in systematic, ecological, and genetic studies of fish (e.g. Butcher 1980; Todd and Smith 1980; Shaklee and Tamaru 1981; Waples 1981; Douglas and Avise 1982), measurement error estimates are an important yet ignored component in morphometric studies (but see Riddell and Leggett 1981).

The use of a digitizing pad to collect morphometric data affords the worker added speed and flexibility in the data collection process. Typically, we can quick-thaw specimens (specimens are frozen for electrophoresis), identify the relevant landmark positions by pinning, and then refreeze the specimens at the rate of 80–100 specimens per 8 h. Landmark information from 80–100 fish can then be digitized in about 90 min. Importantly, tissue preparations from the refrozen specimens can later be subjected to gel electrophoresis for genetic studies without any detectable differences in electrophoretic banding patterns of activity. Hence, a digitizing board approach to morphometric data collection is rapid and facilitates the concurrent use of specimens for morphological and electrophoretic investigations. Moreover, recording X–Y data for relevant landmarks on the outline of a fish provides the fish morphometrician with added flexibility in the selection of traits for analyses without remeasuring specimens. A truss network, a conventional format, or a combination of data types can be rapidly calculated across a body form from the same set of digitized landmarks.

Further study is required to determine whether conventional or truss data sets provide the clearest and most reliable view of shape differences in chinook salmon. A systematic, regionally unbiased network of morphometric measurements over the two-dimensional outline of a fish should provide more information about local body proportions or shape differences than a conventional set of measurements. In the analyses of ontogenetic shape differences in chinook salmon, both data sets indicated the same general pattern of elongation, but analyses of the truss characters indicated that the changes were primarily in the caudal peduncle region. Since the elongation may be associated with smoltification, the localized changes may be associated with the morphological adaptation of smolts preparing for downstream migration. Although truss characters best identify localized character changes, the amount of change between the mean values for samples 3 and 4, the presumed

smolt period, is greater with conventional data in both the GAR and SEA samples. In the analysis of the three wild populations of juvenile chinook salmon, the greatest amount of group separation is achieved using the truss data set. For example, in the classification procedure, 90% of the fish could be correctly classified to group using truss data versus 86% for conventional measurements. This better discrimination with truss data may be due in part to the difference in the number of characters, i.e. 26 truss measurements versus 11 conventional measurements. Both the conventional and truss measurements were calculated from the same set of digitized landmarks; therefore, truss measurements seem to be the most efficient use of a set of digitized landmarks for stock discrimination purposes.

These new multivariate perspectives of geographic and ontogenetic shape variability in chinook salmon are applicable to several active areas of salmon research. A large proportion of the chinook salmon fishery in the Pacific Northwest is dependent on hatchery-reared fish. The capability to predict the release time of hatchery-reared fish, to maximize survival and return to a fishery, is highly desirable in present-day salmon culture (Mahnken et al. 1982). To date, the best potential indicators of smolt or release readiness of hatchery fish are based on physiological or biochemical tests on sacrificed fish (Folmar and Dickhoff 1980). If the changes in shape in early development, as quantified above, are coincidental with other presumptive smolt indicators, then a quickly executed procedure could be devised for use on living (i.e. anesthetized) specimens and tested as a hatchery tool. Though condition factor changed in parallel with SPC II changes in the development studies, and is easy to calculate for individual fish, SPC II values (based on truss data) are less sensitive to daily variation in feeding regimes and rates than the condition factor (G. A. Winans and R. Nishioka, unpubl. data).

The intensive hatchery rearing of chinook salmon and other salmonids has also led to a situation where various stocks or populations are mixed at periods in the life history of the species when fisheries biologists need to distinguish separate populations, as in downstream smolt migrations (Sims and Miller 1982) or in ocean fisheries (Allendorf and Utter 1979). The use of electrophoretic data for mixed stock analyses in the latter instance has been demonstrated (Grant et al. 1980; Milner et al. 1981). Work in related fields of research has shown that morphological data used in concert with measures of electrophoretic data can sharpen our views of character and population varibility (e.g. Spielman and Smouse 1976; Johnson and Mickevich 1977; McGlade and MacCrimmon 1979; Casselman et al. 1981; Winans 1980b). Here, the notion of using measures of multivariate morphometric variation to discern stock differentiation of juvenile chinook salmon is first tested. Additional research is required to determine the best method to incorporate morphometric measurements with electrophoretic data for mixed-stock analysis.

Acknowledgments

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Insights from the Markets for Limited Entry Permits in Alaska

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Under Alaska's entry limitation program, transferable permits convey fishing rights. Information from permit markets is used to study several key issues regarding the behavior of fishermen and the effects of fishery management policy. I conclude that (1) expectations of future fishing incomes are the primary determinants of permit prices, (2) Alaska Department of Fish and Game forecasts of fish recruitment are capitalized in permit values, (3) a state program that provides low-interest loan money to some purchasers of permits has coincided with a significant increase in permit prices, (4) the "average memory" of fishermen in projecting future incomes is about 2.5 yr, and (5) it is possible to infer the rate at which the markets discount future fishing income flows.

En vertu du programme de limitation des inscriptions de l'Alaska, les permis transférables donnent droit à la pêche. Les informations relatives aux marchés de ces permis servent à l'étude de plusieurs questions clés touchant le comportement des pêcheurs et les effets de la politique de gestion des pêches. Je conclus que : (1) l'espérance des gains futurs est le principal facteur déterminant le prix des permis, (2) la valeur des permis traduit les prévisions de recrutement de poisson du *Department of Fish and Game* de l'Alaska, (3) un programme de l'État accordant des prêts à faible intérêt à certains acheteurs de permis a coïncidé avec une augmentation appréciable du prix de ces derniers, (4) la "mémoire moyenne" des pêcheurs lors de la prévision des revenus porte sur environ 2,5 années et (5) il est possible d'établir dans quelle mesure le marché des permis anticipe les revenus futurs de la pêche.

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In 1973 the State of Alaska passed into law an entry limitation program that has now been applied to all commercial salmon (*Oncorhynchus*) and several Pacific herring (*Clupea harengus pallasi*) fisheries (Alaska Statutes 16.43.010 et seq.). Earlier writers have commented on the program's background, motivation, and implementation (Morehouse and Rogers 1980; Adasiak 1979; Rogers 1979). This paper reports on the subsequent developments in markets for limited entry permits. The central thesis of this paper is that, since these permits convey the right to fish,[1] the prices at which they trade convey otherwise unavailable information on several important issues, including (1) fishermen's incomes since entry limitations, (2) how fishermen form expectations of fishing income, (3) the impact of fish run forecasts made by the Alaska Department of Fish and Game, (4) the effects of a state program that provides loans for the purchase of permits at low-interest rates, and (5) the risk premium associated with fishing investment.

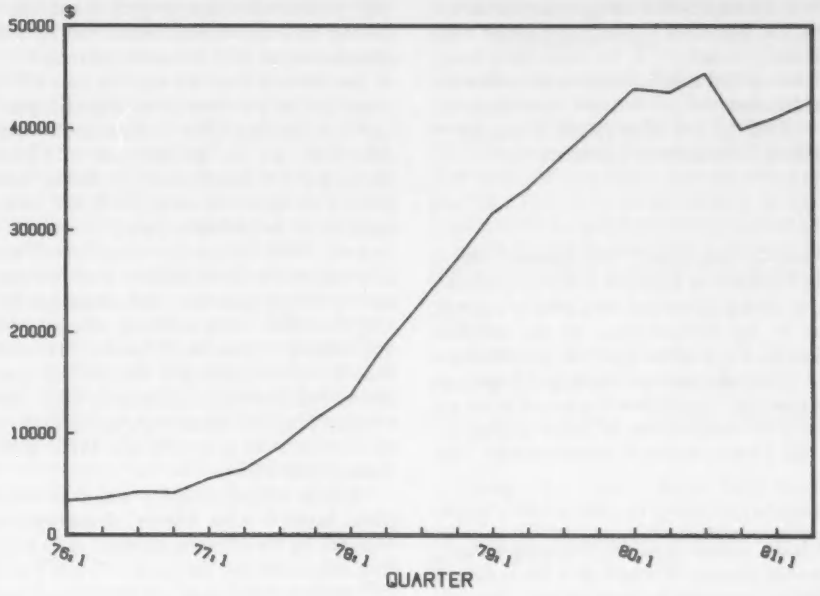
The approach used here is to treat limited entry permits as (non-financial) capital assets. The theory of capital asset pricing is then combined with data on permit prices, fishing incomes, and assumptions of how fishermen form expectations of future income. The first test reported here examines the influence of several key variables on the annual *change* in permit prices. To do this, a simplified theory is used, based on the assumption that fishermen take only their most recent experience to make projections for future years. Although this requires naive or myopic behavior, the model generates some useful conclusions when applied to the data. The second test examines permit price *levels*. This allows the construction of a slightly more complex and realistic model of the expectation process, and adds to the insights of the first test.

Permit prices, in general, increased at a dramatic pace from the initiation of the program in 1975 through 1979, then at a slower (and, at times, negative) rate through the middle of 1981. This is displayed in Fig. 1, which is a plot of the quarterly averages of a weighted index of permit prices from the first quarter 1976 through the second quarter of 1981. On a monthly basis, the index W_t is computed as

$$W_t = \frac{\sum_f n_{ft} P_{ft}}{\sum_f n_{ft}}$$

where the n_{ft} is the number of outstanding (permanent) permits in fishery f at date t and P_{ft} is a measure of the market price of a permit in fishery f at date t. One of the more lucrative fisheries, the Chignik purse seine fishery, is excluded from the index because of a lack of monthly data, so the index has a slight

[1]Legally, each permit conveys the "privilege" to fish. The distinction between "rights" and "privileges" is important in that the latter is more easily revoked by state decree. Nevertheless, I will use the more common term "right" to denote one's legal access to a fishery.



downward bias. The index stood at $3557 (U.S.) in June 1976 and $45 501 in June 1981, which represents an average annual growth rate of about 66%. Since it is an average, it obscures even more dramatic increases and price levels in many fisheries.

Data

Data from several sources were combined in the statistical tests reported below. The result was a pooled set of cross-section and time-series data on 14 fisheries for each of the 6 yr 1976–81. (The 14 fisheries are (a) purse seine: Southeast Alaska, Prince William Sound, Cook Inlet, Kodiak, Chignik, and Alaska Peninsula, (b) beach seine: Kodiak, (c) drift gill net: Southeast Alaska, Prince William Sound, Cook Inlet, Alaska Peninsula, and Bristol Bay, and (d) set gill net: Kodiak and Alaska Peninsula.) Because of occasional missing data, the sample was reduced to 57 cases for the test in part I and 67 cases for the test in part II.

Permit price data were collected from the Alaska Commercial Fisheries Entry Commission's survey file on permit transfers. As the administrating agency of the limited entry program, the Alaska Commercial Fisheries Entry Commission collected voluntary survey data from permit transferors and transferees. (The survey is now mandatory.) Net income data were estimated in three steps. (For a detailed discussion, see Karpoff 1983, Appendix 1). First, an Alaska Commercial Fisheries Entry Commission file of vessel harvests and revenues was used to estimate gross fishing revenue by vessel in each fishery. The Alaska Commercial Fisheries Entry Commission data were in turn based on "fish ticket" catch data collected by the Alaska Department of Fish and Game. Second, data from a 1979 survey conducted jointly by the United Fishermen of Alaska and the Alaska Sea Grant Program (see Larson 1980) were used to estimate the relation between gross revenues and costs. This was applied to the gross fishing revenue of the previous step to estimate "net incomes" for each vessel in each year. And third, the "net income" of the marginal permit holder was estimated for each fishery in each year using a procedure that is described in Karpoff (1983, Appendix 1). Economic theory predicts that market prices reflect the demand-price of the marginal permit holder, so these "marginal net income" figures were used for the variables $\Delta\pi$ and π in the tests that follow.

Finally, three variables are used in this paper that were constructed to measure the informational content of the annual forecasts made by the Alaska Department of Fish and Game about the coming season's stock recruitment. Because the development of these measures was rather crude, they are described in greater detail in the text below. The raw data used to construct these three measures (DEVF, FERROR, and NFR) were obtained from various Alaska Department of Fish and Game publications from 1974–82. Each publication generally contains recruitment and/or harvest data for an individual species in a geographic area for the most recent fishing season, as well as recruitment forecasts and/or harvest projections for the coming season.

I. Permit Price Movements

Methods

Consider the following model of a limited entry permit price. If permits are treated as capital goods, an individual fisherman's demand-price for a permit is the present value of the income stream that is expected to accrue from fishing:

$$(1)\qquad P^i_{ft} = \sum_{k=0}^{\infty} \frac{E^i_t(R^i_{f,t+k}) - E^i_t(C^i_{f,t+k})}{\{1 + E^i_t(r^i_{f,t+k})\}^k}$$

where P^i_{ft} = the ith individual's demand-price for a permit in fishery f at date t, $E^i_t(R^i_{f,t+k})$ = the ith individual's expected revenues earned in fishery f at date $t + k$, the expectation being formed at date t, $E^i_t(C^i_{f,t+k})$ = the ith individual's expected *total* costs (exclusive of the permit) incurred from fishing in

fishery f at date $t + k$, the expectation being formed at date t, and $E^i_t(r^i_{f,t+k})$ = the ith individual's expected relevant risky discount rate for fishery f at date $t + k$, the expectation being formed at date t. In the special case in which expectations are that profits and the discount rate are constant over time, i.e. where $E^i_t(R^i_{f,t+k}) - E^i_t(C^i_{f,t+k}) = E^i_t(\pi^i_f)$ and $E^i_t(r^i_{f,t+k}) = E^i_t(r^i_f)$ for all k, equation (1) reduces to a perpetuity:

$$(2) \quad P^i_{ft} = \frac{E^i_t(\pi^i_f)}{E^i_t(r^i_f)}.$$

The number of permits in each fishery is determined exogenously by the Alaska Commercial Fisheries Entry Commission at a number, say L_f, so the equilibrium market price of a permit in fishery f, equal to the demand-price of the marginal fisherman, is simply $P^{L_f}_{ft}$. The superscripts will henceforth be dropped, and P_{ft} will refer to the market-clearing permit price at date t. The model of equation (2) indicates that permit prices are proportionately related to expectations of future fishing incomes, with $\Theta_{ft} = 1/E_t(r_f)$ the constant of proportionality. That is,

$$(3) \quad P_{ft} = \Theta_{ft} \cdot E_t(\pi_f).$$

Permit price levels are examined in the following section. Here, we examine annual changes in permit price levels using a simple theory of how fishermen form future income expectations. Equation (3) implies

$$(4) \quad P_{ft} - P_{f,t-1} = \Theta_{ft} \cdot E_t(\pi_f) - \Theta_{f,t-1} \cdot E_t(\pi_f).$$

Initially, to make the problem tractable, let us assume that fishermen are "myopic" in that they consider only last year's income in their projections of future incomes:

$$(5) \quad E_t(\pi_f) = \pi_{f,t-1}.$$

From equation (4),

$$P_{ft} - P_{f,t-1} = \Theta_{ft}\pi_{f,t-1} - \Theta_{f,t-1}\pi_{f,t-2}.$$

If we further assume that expected discount rates are constant over time and across fisheries, i.e. $E_t(r_f) = r$ for all t and f, this simplifies to

$$(6) \quad \Delta P_{ft} = \Theta \cdot \Delta \pi_{f,t-1}$$

where Δ represents the first-order difference and Θ is the inverse of the (assumed constant) risky discount rate. The assumption that Θ is constant over time and fisheries allows us to pool the short time series (from 1976–81) data from 14 different fisheries in the empirical tests reported below. While rates are probably not much different across fisheries, our assumption may not hold with respect to intertemporal homogeneity. This is because the permit price and income data included in the tests are expressed in current dollars, and nominal interest rates were in general rising over the sample period. This will be a source of caution in the interpretation of the results below.

Before applying this model to the data, four additional influences were considered and variables added. The first was a dummy variable, ELEC, which was designed to distinguish the effect, if any, of a fall 1976 general election ballot initiative that would have, if passed, repealed the limited entry act. Presumably, permit prices would be discounted in 1976, reflecting the uncertainty over the outcome of the ballot initiative. To account for this, the variable ELEC was set equal to 1 for 1976 observations and 0 for all other years. It was expected to have a negative coefficient. The second influence included was the 1979 initiation of a state program to help finance the purchase of permits with low-interest loans. The Alaska State Legislature passed an act in 1978 that allows permits to be used as collateral on low-interest loans through the state's Division of Business Loans for the purchase of permits (Chapter 83, 1978 Session Laws of Alaska). Prior to this, loans could be acquired by fishermen only for the purchase of vessels and gear. The enabling statute had explicitly prohibited fishermen from using permits as legal collateral for loans, and this substantially reduced an individual's ability to finance a permit (Alaska Statutes 16.43.150(g) (1)). The subsidized loans, for which only state residents are eligible, were first made in 1979 at a 7% rate of interest. The rate was increased to 9.5% in 1981 and to 10.5% in 1982. There is reason to believe that the loan subsidy was enacted to favor the entrance of Alaska residents into the fisheries. To the extent the loan subsidy would increase permit prices, nonresidents would merely face a higher cost of entry. For residents, the higher price would be offset by the effective subsidy, and the relatively low price would favor entry by Alaska residents.

The loan subsidy program was expected to increase permit prices because some buyers' demand-prices would now be bolstered by the effective subsidy. As a rough estimate, it has been calculated that the initial 7% rate was sufficiently below 1979 market rates to cause an increase in buyers' demand-prices of up to 34.9% (Karpoff 1984). To capture this anticipated effect, a variable called LOANSTRT (for the start of the loan program) was added to the model. It was constructed to capture the percentage increase in permit prices attributable to the initiation of the loan program:

$$(7) \quad \text{LOANSTRT}_{ft} = D_t P_{ft}$$

where D_t is a dummy variable set equal to 1 for 1979 cases and 0 otherwise and P_{ft} is the permit price in fishery f at date t. The inclusion of P_{ft} in the definition of LOANSTRT does not introduce an error into the subsequent empirical test, since the dependent variable is *the change in* permit prices. Notice also that LOANSTRT is set equal to 0 for years 1980 and 1981, even though the loan program was in effect those years. Again, this is due to the definition of the dependent variable: although the loan subsidy is expected to affect the *level* of prices throughout its life, it was expected to cause an otherwise unaccounted for *increase* in permit prices only upon its initiation. (The effect of the loan subsidy on demand-prices should vary with changes in the spread between market rates and the subsidized low rate. The specification of LOANSTRT in equation (7) abstracts from this by assuming the effect on demand-prices was the same through 1981.)

The third influence added to the model, DEVF, was constructed as a measure of the unexpected change in fish run forecasts provided by the Alaska Department of Fish and Game. Since permit prices reflect in part expectations of future fish runs, and since it is likely that these expectations are at least partially based on Alaska Department of Fish and Game forecasts, it is probable that forecasts that project a change in stock recruitment will cause permit price changes. The measure of DEVF was rather crude, so its complete development is detailed here.

Define the following variables: FR_{ftl} = the forecast return of the salmon species l in the geographic area of fishery f at date t and AR_{ftl} = the actual measured return of the salmon species l in the geographic area of fishery f at date t.

A measure of the change in the expected run of a particular

species is (FR_{ft} − $AR_{ft-1,t}$). For most fisheries, one or two species comprise the bulk of the catch, although other species may be caught in smaller numbers. Also, the Alaska Department of Fish and Game may provide forecasts for only one or two species in each geographical area. For these reasons, it was possible to establish one measure each of forecast return (FR_{ft}) and actual return (AR_{ft}) even though all five North Pacific salmon species may be harvested in a given area. In those areas where only one species' run was forecast, this was taken as the measure of FR_{ft}. If two species' run was forecast, the forecast variable was computed as the sum of the individual species' forecasts. Actual returns were computed the same way. To prevent any error from adding, say, a forecasted pink salmon (*Oncorhynchus gorbuscha*) run to a forecasted sockeye salmon (*O. nerka*) run, the variables FR_{ft} and AR_{ft} were weighted by the average price per fish captured. Without this adjustment, a large forecast change in a higher valued species (e.g. sockeye salmon) would be assigned no more weight than a similar forecast change in a lower valued species (e.g. pink salmon). So two new variables were created, the value of the forecast return (VFR_{ft}) and the value of the actual return (VAR_{ft}), where

$$VFR_{ft} = FR_{ft} \cdot PPF_{ft}$$

$$VAR_{ft} = AR_{ft} \cdot PPF_{ft}$$

and PPF_{ft} = the average price per fish harvested in fishery f at date t. Weighting by the average price per fish allows an increased harvest (or projected harvest) of a higher valued species to be reflected in a relatively higher value of VAR_{ft} (or VFR_{ft}), since the relatively larger run of the higher valued species will cause a higher average price per harvested fish. Likewise, changes in forecast or actual runs of lower valued fish will have smaller relative impacts on VFR_{ft} and VAR_{ft}, since the proportionately greater number of lower valued fish will cause a relative decrease in PPF_{ft}. Note that the *forecast* return is weighted by the *actual* price per fish for a given year. This is for two reasons. First, there is a positive correlation between forecast and actual runs, so a forecast change of a particular species' run correlates with an actual change, and the average price per fish is affected accordingly. Second, fish price agreements between fishermen and processors are generally made before the actual capture of fish, and usually before the beginning of the fish run. So even if the actual return deviates from the forecasted return, fish prices paid to fishermen will largely reflect the size of the forecast run.

Finally, the measure of the change in the expected value of the fish run ($DEVF_{ft}$) was created as the difference between the value of the forecast return and the lagged value of the actual return:

(8) $DEVF_{ft}$ = the change in the expected value of the fish run

$$= VFR_{ft} - VAR_{f,t-1}.$$

It was expected that a change in the value of this variable would cause a change in the permit price in the same direction.

The fourth variable entered into the model of equation (6) was an attempted measure of the informational content of the Alaska Department of Fish and Game's forecast. The historical accuracy of these forecasts varies over geographical areas, with prediction errors of 50% or more common in some areas. It is unlikely that a forecast that has been unreliable in the past would provide as much new information, since fishermen are likely to discount any news of forecasted changes. To account for this, a variable was created to measure the inaccuracy of the most recent forecast, called FERROR for "forecast error":

(9) $FERROR_{ft} = |(AR_{f,t-1} - FR_{f,t-1})/AR_{f,t-1}|$

where the vertical bars indicate that absolute values were taken. It was expected that FERROR would correlate negatively with permit price changes, reflecting the extent to which the effect of DEVF is discounted. Note that this hypothesis is valid only as joint with the hypothesis that the effect of DEVF on ΔP is positive. That is, a positive effect of DEVF is a necessary condition for the suspected negative effect of FERROR. Also, it is assumed that a forecast error adds uncertainty to a subsequent forecast regardless of the direction of error.

Results

Combining the four additional variables to the model of equation (6) provides the complete model:

(10) $\Delta P_{ft} = g(\Delta\pi_{f,t-1}, ELEC_t, LOANSTRT_t, DEVF_{ft}, FERROR_{ft})$.

Testing the model in linear form provided the following ordinary least squares fit (t-statistics are in parentheses; *significant at the 0.01 level, **significant at the 0.10 level; R^2 = 0.59, F = 14.61, df = 51):

$$\begin{aligned}(11)\quad \Delta P_{ft} = {} & 7601 + 1.49\Delta\pi_{f,t-1} - 6700ELEC_t \\ & (3.63)^* \quad (6.43)^* \quad (-1.71)^{**} \\ & + 0.23LOANSTRT_t + 0.11DEVF_{ft} - 581FERROR_{ft}. \\ & (3.56)^* \quad (1.87)^{**} \quad (-0.24)\end{aligned}$$

The coefficients all have signs as expected, and with the exception of FERROR are statistically significant at the 10% level. The coefficient on ELEC suggests that permit prices were discounted in 1976. However, further tests revealed that this result may not be caused by the 1976 initiative on limited entry. As reported in the Appendix, tests that entered a dummy variable for 1977 also obtained a negative coefficient. This is contrary to what I expected, since, if permit prices were discounted in 1976 because of uncertainty over the initiative to abolish limited entry, the defeat of this issue would cause an increase in 1977 prices. Further tests reported in Karpoff (1983) indicate that 1976 and 1977 residuals were often negative, suggesting a possible structural break in the data between 1977 and 1978. One explanation of a structural break is the Fisheries Conservation and Management Act, which established a 200-mi (322 km) offshore limit to United States jurisdiction and decreased nearshore competition from foreign vessels. To the extent fishermen anticipated the resulting benefit to them, permit prices would increase. But this would have shown up in 1976 and 1977 prices, since the Fisheries Conservation and Management Act was passed in the spring of 1976. Another explanation suggested in Karpoff (1983) is simply that permit markets were relatively disorganized in the early years of the program, and that because of high information and/or transaction costs, many exchanges were made at less than "competitive" prices.

Whatever the cause of a suspected structural break between 1977 and 1978, one thing must be emphasized: in all tests, including those that tested for structural break and those reported in the Appendix, the coefficients on $\Delta\pi$, LOANSTRT, and DEVF were nearly identical in magnitude and statistical significance. So we may derive inferences from these with some amount of confidence.

More will be said about these results later, but we summarize

them now. The coefficient on LOANSTRT indicates that an increase, not otherwise explained, occurred in permit prices during the first year that permits could be financed with low-interest loans. Because of the definition of this variable (equation (7)), this increase is interpreted as an average of 23% of a permit's 1979 value. Note that this accounts for differences in the effect of the loan subsidy for different amounts likely to be financed. The absolute price increase is higher for higher valued permits, since more can be financed at below-market rates, and lower for low-priced permits.

The coefficient on DEVF suggests that permit prices are revised in accord with Alaska Department of Fish and Game projections. The coefficient on FERROR suggests that this effect is strongest where Alaska Department of Fish and Game forecasts have been most accurate, but this coefficient is not statistically different from zero. The differences in the magnitudes of the coefficients on DEVF and FERROR result from the differences in the magnitudes of their measurements. FERROR is measured as a percentage and rarely assumes a value with absolute value greater than two, whereas DEVF is measured in absolute (dollar) terms and is often a large number because FR and AR are large numbers.

The coefficient on $\Delta\pi$ indicates that permit prices do change with recent fishing experience. But its low value, combined with the large intercept term and low R^2 value, suggests that a significant portion of permit price behavior is not captured by this model. In part II, a more complex model of fishermen's expectation process is employed with greater success.

II. Permit Price Levels

Methods

Equation (3) states that permit prices are a function of long-term income expectations:

$$(12)\quad P_{ft} = \Theta \cdot E_t(\pi_f)$$

where the assumption of a constant discount factor Θ is maintained from the previous section. To model $E_t(\pi_f)$ in this section, an adaptive expectations model is developed along the lines of some models used in the analysis of consumer behavior. (A "rational expectations" operator, Alaska Department of Fish and Game forecasts, is added to the model below.) Because of its similarity to Friedman's exposition of the permenant income hypothesis (Friedman 1957) and because the net income that accrues from fishing is often labelled rent, this model is called the "permanent rent hypothesis." Strictly, economic rent refers to the price of a "nonaugmentable" good over and above its supply-price. The stock of fish is augmentable, so we may more accurately refer to a fishery's "quasi-rent." Either way, this refers to the value of the harvested fish minus the cost of the least cost method of harvesting. Intuitively, this quasi-rent is the value of the natural resource itself. $E_t(\pi_f)$ is a measure of long-term "permanent" income (rent) currently expected by the marginal fisherman in fishery f. It is hypothesized that, to arrive at his expected permanent rent, a fisherman will revise his previous period's expectation by some proportion of its deviation from last period's realized income. Dropping the f subscripts to simplify the exposition,

$$E_t(\pi) - E_{t-1}(\pi) = \beta(\pi_{t-1} - E_{t-1}(\pi))$$

or

$$(13)\quad E_t(\pi) = \beta\pi_{t-1} + (1-\beta)E_{t-1}(\pi)$$

where β is the "expectations adjustment parameter," $0 < \beta < 1$. Lagging equation (13) one period,

$$E_{t-1}(\pi) = \beta\pi_{t-2} + (1-\beta)E_{t-2}(\pi).$$

Equation (13) may then be expressed as

$$E_t(\pi) = \beta\pi_{t-1} + \beta(1-\beta)\pi_{t-2} + (1-\beta)^2 E_{t-2}(\pi).$$

Continuing this recursive process backwards implies that

$$(14)\quad E_t(\pi) = \beta \sum_{j=0}^{\infty} (1-\beta)^j \pi_{t-1-j}.$$

Expected permanent rent is expressed as a function of past realized fishing incomes. Letting $\lambda = 1 - \beta$, λ is a measure of how heavily past experiences are weighted in forming future expectations. A high λ implies a long memory; a low λ implies that $E_t(\pi)$ is revised substantially in accord with recent experience.

Substitution of equation (14) into equation (12) gives

$$(15)\quad P_t = \Theta(1-\lambda) \sum_{j=0}^{\infty} \lambda^j \pi_{t-1-j}.$$

This may be transformed into estimatable form by the method first used by Koyck (Evans 1969, p. 23). From equation (15),

$$(16)\quad \lambda P_{t-1} = \Theta(1-\lambda) \sum_{j=0}^{\infty} \lambda^{(j+1)} \pi_{t-j-2}.$$

Subtracting equation (16) from equation (15),

$$P_t - \lambda P_{t-1} = \Theta(1-\lambda)\pi_{t-1}$$

or

$$(17)\quad P_t = \Theta(1-\lambda)\pi_{t-1} + \lambda P_{t-1}.$$

Equation (17) is the mathematical expression of the "permanent rent hypothesis." It states that in the absence of other important factors, permit prices can be expressed as functions of their lagged values and lagged net revenues, with no intercept term. Note that this model incorporates one of many possible distributed lag structures to model expectations. We need not assume that the fishermen consciously formulate future expectations according to this model. But to the extent that it fits the data and proves predictively accurate, the model is useful.

However, it is hypothesized that at least two other factors are important in permit pricing. The first is a measure of how permit prices should also reflect future expectations of fish harvests. That is, in addition to past experiences and adaptive expectations, we would expect fishermen to weigh expectations of future harvests in their demand-prices for permits. This was done by establishing a variable that attempts to measure the effect of Alaska Department of Fish and Game forecasts of fish runs.

Because it measures *changes* in the value of fish run forecasts, the variable DEVF as developed in part I would be an inappropriate measure of the effect on permit price *levels*. But since fish runs vary by quantity and species across fisheries, entering the absolute level of fish run forecasts would also provide erroneous results about the effects of fish run forecasts. For example, a projected increase of 1 000 000 fish would be assigned greater weight than a 750 000 fish increase. But if the former increase were of pink salmon and the latter of sockeye salmon, it is likely that the latter, being of a more valuable species, would have a greater impact on permit prices. To correct for this, a measure of "normalized" fish run forecasts was created to capture the *relative* optimism of a given year's

forecast compared with other years. Called NFR, it is equal to the percentage deviation from the mean forecast over the years 1974–81:

$$\mathrm{NFR}_{ft} = \frac{\mathrm{FR}_{ft} - \overline{\mathrm{FR}}_f}{\overline{\mathrm{FR}}_f}$$

where $\overline{\mathrm{FR}}_f$ is the mean forecast from 1974–81. Since this measure is unique to each fishery, it does not have the problem of comparing forecasts of different species over different fisheries.

To estimate the effect of the loan program, a dummy variable called LOANEFF was created and set equal to 1 for years in which the loan program was in operation and 0 for all other years. This is a crude measure, for unlike the LOANSTRT variable of the previous section, it could not be constructed to account for differences in the value of the loan subsidy that arise from differences in prices of permits being financed by the subsidy. In addition, the effective loan subsidy should be expected to change over time as the difference between the relevant market and subsidized interest rates change. So, although the estimated coefficient on LOANEFF is interpreted below as the increase in price of the hypothetical average permit due to the loan subsidy, it is expected that much cross-sectional and inter-year variation in this effect is obscured in this single estimate.

Because of their statistical weakness in price movement tests, FERROR and ELEC were not entered. The equation estimated, then, had the form

$$(18)\quad P_{ft} = \Theta(1-\lambda)\pi_{f,t-1} + \lambda P_{f,t-1} + b_1\mathrm{NFR}_{ft} + b_2\mathrm{LOANEFF}_t + e_{ft}$$

where Θ, λ, b_1, and b_2 are parameters of the model and e_{ft} is a random error term.

Results

The estimation of equation (18) involves statistical problems that arise from the underlying adaptive expectations model and its transformation into estimatable form. At issue is the distribution of the random error term. Fortunately, the application of ordinary least squares is perhaps the most defensible way of handling these problems. At the very least, ordinary least squares provides estimates that approximate those derived from more complex statistical techniques (Karpoff 1983, Appendix 3). Equation (19) reports the ordinary leasts squares results (t-statistics are in parentheses; *significant at the 0.01 level, **significant at the 0.10 level; $R^2 = 0.944$, $F = 266.78$, df = 63):

$$(19)\quad P_{ft} = \underset{(8.16)^*}{1.72\pi_{f,t-1}} + \underset{(8.37)^*}{0.76P_{f,t-1}} + \underset{(2.27)^{**}}{6050\mathrm{NFR}_{ft}} + \underset{(1.91)^{**}}{8242\mathrm{LOANEFF}_t}.$$

The estimate $\hat{b}_2 = 8242$ can be interpreted as the average effect on a hypothetical average permit of the state loan subsidy program on permit prices over the years 1979–81. The estimate is statistically significant at the 5% level (using a one-tailed test) and it supports the estimated coefficient on LOANSTRT in equation (11). The average value of the weighted permit price index during 1979, a measure of a hypothetical "average" permit price, was $35 896; 23% of this is $8256. This provides an upper bound estimate of the average effect predicted by the equation (11) estimate. A lower bound estimate is derived by treating $35 896 as the end product of a 23% increase: $(1 + 0.23)P_0 = \$35\,896$, and P_0, an estimate of permit prices in the absence of the loan program, is $29 184. Twenty-three percent of this is $6712. So the equation (11) estimate, together with the weighted permit price index, predicts a value of b_2 of between $6712 and $8256. And $\hat{b}_2 = \$8242$, so we have two separate tests of the effect of the loan program that are mutually supportive and extremely close in their point estimates.

The estimate $\lambda = 0.76$ (or $\beta = 0.24$) can be used to make inferences about the average length of the marginal fisherman's "memory." Expected permanent rent, expressed solely as a weighted average of past realized fishing income, is

$$E_t(\pi) = 0.24\pi_{t-1} + 0.18\pi_{t-2} + 0.14\pi_{t-3} + 0.11\pi_{t-4} + 0.08\pi_{t-5} + 0.06\pi_{t-6} + \ldots$$

Since the sum of the weights equals 1,[2] one half of the weights is accounted for by counting back 2.56 yr. "This is the average time lag between the estimated permanent (rent) and the observations from which it is estimated ..." (Friedman 1957, p. 145; see also Griliches 1967, p. 19). A large λ would have implied a longer average retrospective time span in the derivation of expected permanent rent, and a smaller λ a shorter span. As it is, our estimate of 2.56 yr is very close to the 2.5-yr estimate obtained by Friedman in his consumption behavior analysis. In their anticipation of long-term expected fishing income, it appears that fishermen are not unlike consumers considering their long-term expected (permanent) incomes.

The estimate $\Theta(1 - \lambda) = 1.72$, together with $\lambda = 0.76$, implies an estimate of $\Theta = 7.167$, which in turn provides an empirical estimate of the risky discount rate appropriate to fishing investment. Recall that $\Theta = 1/r$, where r is the (assumed constant) risky discount rate appropriate to fishing. Then an estimate of r is $\hat{r} = 1/7.167 = 13.95\%$. This seems intuitively plausible, but it must be interpreted with caution. The data used to estimate equation (19) span 6 yr, 1976–81. Price and income data were not deflated, so $\hat{r}$ is a measure of an "average" nominal discount rate for fishing. Nominal interest rates in general fluctuated during this time, from a low of 4.98% for a United States' 3-mo Treasury Bill in 1976 to a high of 14.65% for the first 6 mo of 1981. The average nominal 3-mo T-bill rate during this time period was 8.90%, 5.05 percentage points lower than 13.95%. By treating the T-bill rate as a measure of the "riskless" rate, this provides an estimate, however crude, of the risk premium associated with fishing investment. (At least one Seattle bank provides fishing-related loans at prime plus two percent to "good customers." This is very close to our estimate of a total risk premium of 5.05%.)

Discussion

The results of tests for both *changes in* and *levels of* limited entry permit prices may be grouped by the following five "insights":

(1) Fishing Income

Permit prices correlate strongly with measures of the profitability of fishing. Regardless of any other aspects unique to the

[2]From equation (14), the weight assigned to π_{t-1-j} is $\beta(1-\beta)^j$, and the sum of these weights for all j is $\beta\Sigma_{j=0}^{\infty}(1-\beta)^j = \beta[1/(1-(1-\beta))] = 1$.

fishing industry, it appears that fishermen price permits in the same manner that business people price all capital assets: by referring to the discounted present value of the asset.

(2) Alaska Department of Fish and Game Forecasts

It appears that fish run forecasts provided by the Alaska Department of Fish and Game affect permit prices, presumably because they affect expectations of the future profitability of fishing. One test indicates that about 11% of the *change* in a measure of the expected value of the fish run is reflected in permit price changes. A second test estimates that a one percentage point deviation in the fish run forecast from a long-term average correlates with a $60.50 increase (for positive deviations) or decrease (for negative deviations) in permit price levels. It is suspected that the effect of these forecasts is moderated by previous Alaska Department of Fish and Game errors. That is, new information is readily used where the department has previously been accurate, but is discounted to the extent that previous forecasts have been wrong. However, the tests employed here could not detect any such discounting.

(3) Low-Interest Loans

The availability of low-interest loan money through the state's Division of Business Loans correlates strongly with an otherwise unexplained increase in permit prices. One test measured an average 23% increase in permit prices in 1979, the year immediately following the legislation that enabled the loan program, an increase *over and above* that which may be attributed to optimism about the 1979 and future fishing seasons. This was confirmed by a second test that indicates that, averaging over all permits during the life of the loan program, prices were $8242 higher than they otherwise would have been.

(4) Retrospective Time Horizon

Tests for permit price levels confirm the notion that prices are revised in accord with experience, since past experiences influence expectations of the future profitability of fishing. Specifically, it appears that the average time span considered in forming expectations of future fishing incomes is 2.56 yr. That is, fishermen consider their experiences of the past two to three fishing seasons most strongly in their projections for future years. This estimate is surprisingly close to those obtained in other analyses of how consumers formulate their long-term income expectations.

(5) Risk Premium

Over the 5.5-yr period covered by the data, the average revealed nominal risky discount rate appropriate to fishing was estimated at 13.95%. However, this is a rough estimate, since it involves averaging over time and across fisheries.

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Appendix

Here, two alternative specifications of equation (10) are reported in which a dummy variable for 1977 observations was entered. Because of the defeat of the 1976 initiative to abolish limited entry and the 1976 enactment of a "200-mi limit" in the United States, the coefficient on the 1977 dummy was expected to be positive. The fact that it turned up negative led to suspicions, discussed briefly in the text, that some unmodelled factor was affecting 1976 and 1977 data.

TABLE A.1. Regression coefficients for alternative formulations of tests for permit price movements (equation (10)). Dependent variable = ΔP_t, t-statistics in parentheses).

Variable	Eq. (A.1)	Eq. (A.2)
$\Delta\pi_{t-1}$	1.47 (6.53)	1.56 (6.76)
LOANSTRT$_t$	0.19 (2.86)	0.24 (3.60)
DEVF$_t$	0.14 (2.29)	0.11 (1.75)
FERROR$_t$	2041 (0.76)	1580 (0.57)
ELEC$_t$	−9166 (−2.31)	—
DUMMY77$_t$	−8238 (−2.12)	−5620 (−1.46)
Constant	8970 (4.22)	6651 (3.41)
R^2	0.62	0.58

Univoltine and Semivoltine Life Histories in *Senecella calanoides* (Copepoda: Calanoida) and Their Relationship to Body Size

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Most populations of *Senecella calanoides* Juday in eastern Canada are univoltine. However, in Lake Mazinaw, southern Ontario, and probably in three additional lakes in western Quebec it has a 2-yr life history (semivoltine) with two fractions, different in age by 1 yr, developing together. The additional year of development in Mazinaw is spent almost entirely in the fourth and fifth copepodite instars. Slower development in semivoltine populations is tentatively attributed to colder waters resulting from extensive hypolimnia, with limited food as a possible secondary cause. Later copepodites of semivoltine populations were smaller than their univoltine counterparts, possibly because of poorer nutrition.

La plupart des populations de *Senecella calanoides* Juday de l'est du Canada sont univoltines. Le lac Mazinaw du sud de l'Ontario et, sans doute, trois lacs de l'ouest du Québec contiennent cependant des individus à cycle biologique biannuel (semivoltins) répartis en deux groupes, dont l'âge diffère de 1 an, se développant côte à côte. L'année supplémentaire de développement dans le lac Mazinaw se passe presque entièrement sous la forme de copepodite de quatrième et cinquième stades. On émet l'hypothèse que le développement plus lent des populations semivoltines s'explique par des eaux plus froides résultant d'un important hypolimnion et, peut-être aussi, par la rareté de nourriture. Les dernières copépodites des populations semivoltines étaient plus petites que leurs correspondantes univoltines, ceci peut-être à cause d'une moins bonne alimentation.

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The calanoid copepod, *Senecella calanoides* Juday, is the only member of the Pseudocalanidae found in freshwaters. Its distribution is confined to northern North America, a limited area of eastern Siberia (Slastnikov 1940), and brackish regions of the Arctic Ocean off northern Siberia (Pirozhnikov 1958). In northeastern North America it occurs only within the area formerly occupied by glacial lakes or their spillways (Dadswell 1974; Carter et al. 1980) and is therefore usually considered a glacial relict or glacial opportunist.

Senecella calanoides is one of the largest freshwater calanoids with a total length of about 3 mm. It is usually found only in the hypolimnia of lakes of moderate to great depth and is consequently often regarded as a cold-water stenotherm. However, it often ascends into warm waters at night and it is possible that its daytime residence at depth is partly a tactic to avoid piscine predators. Present knowledge of its feeding behavior suggests that it is a filter-feeding omnivore consuming diatoms and other algae as well as small zooplankters such as nauplii (G. Sprules, Erindale College, University of Toronto, pers. comm.).

Senecella calanoides is univoltine in Parry Sound, Ontario (Carter 1969). To investigate the generality of this pattern we examined *S. calanoides*' life histories in lakes with different thermal and biotic conditions in Ontario and Quebec. In this paper we document both univoltinism and semivoltinism and attempt to identify factors determining 1- or 2-yr life cycles. We also discuss the relationship between type of life cycle and copepodite cephalothorax lengths.

Methods

We had available multiple samples from 3 lakes (Parry Sound, a semi-enclosed basin of Georgian Bay, Charleston, and Mazinaw) and single samples from 54 lakes in Ontario and Quebec. The three multiple-sample lakes were placed together as the southern Ontario set, based on similarity of latitude (Fig. 1). Of the single-sample lakes, 10 fell naturally into two sets, Abitibi and Gatineau, based on geographical proximity and, in most cases, nearness in sampling time (Fig. 1). The remaining 44 lakes, while the samples were analyzed, were left ungrouped and will be mentioned only briefly in the study.

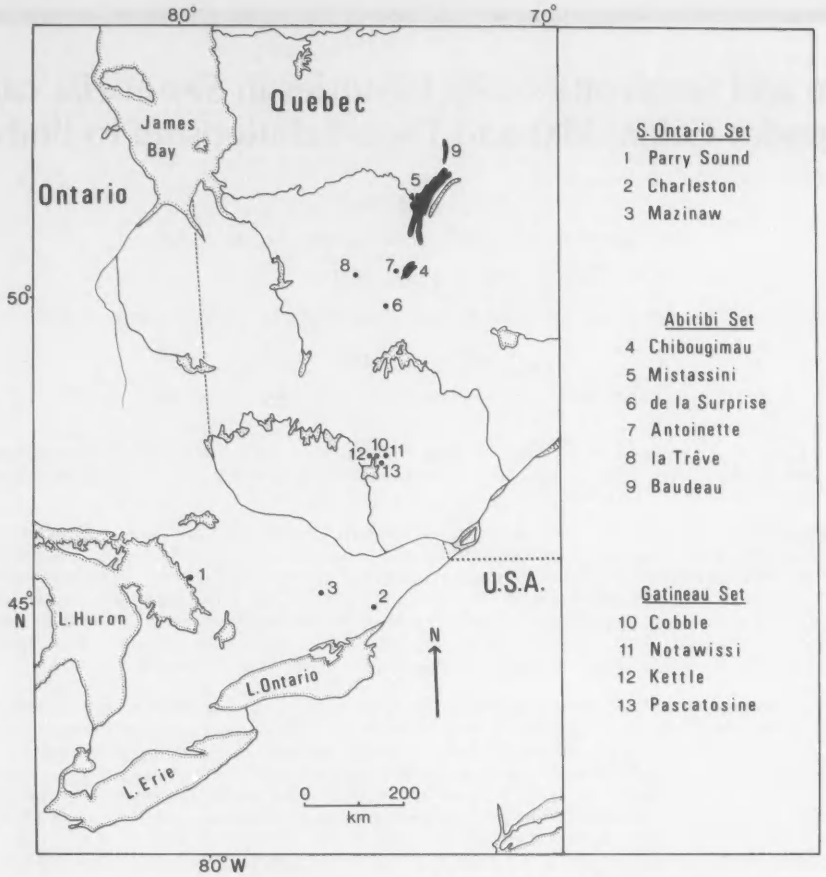

FIG. 1. Eastern Ontario and western Quebec with locations of the 13 lakes.

Lake Mazinaw, was sampled between June 1981 and February 1983 at a single station, 52 m deep. Collections were made at approximately 2-wk intervals from June to November 1981, February to July 1982, and late January to late February 1983; during intervening periods, sampling was less frequent. Lake Charleston was sampled once in each of June and August 1981 at a single station 88 m deep. On all occasions in both lakes three vertical hauls with a conical net of 0.5 m mouth diameter and No. 25 nylon mesh (apertures 64 μm) were made from bottom to surface.

In the laboratory, three 25-mL subsamples were extracted from each well-mixed sample and the copepodite instars and nauplii were counted. From Mazinaw at least 500 individuals and from Charleston at least 300 individuals were enumerated for each sampling date. The mean abundances per sample for each triplicate sample were then calculated.

The life cycle in Parry Sound was adapted from Carter's (1969) study. The remaining samples were collected by Dadswell between 1969 and 1972 from the series of lakes indicated in Carter et al. (1980). During that period Charleston was sampled seven times and all other lakes once. In each instance a single bottom to surface haul was taken from the deepest point in each lake with a conical net of 0.32 m mouth diameter and No. 6 nylon mesh (apertures 239 μm). In most of these lakes *S. calanoides* was not abundant and the entire sample was counted. In a few lakes, including Charleston where it was very common, a minimum of 200 individuals was counted.

Cephalothorax length measurements were made with an ocular micrometer of 20 individuals of each copepodite of all generations in lakes of the southern Ontario set except the first generation in Parry Sound of which many animals had been destroyed; measurements of 20 individuals (occasionally less) were also made of each copepodite instar from the single-sample lakes.

The nauplii of *S. calanoides* have never been described and as it was unnecessary for the present study to separate them into instars, they were grouped simply as "total nauplii." Furthermore, they invariably appeared to be somewhat undersampled, even with a No. 25 net: the eggs presumably hatch on the bottom sometime after being extruded individually by the female, and it is very likely that many of them remain too close to the sediments to be captured by a plankton net.

To facilitate graphical representation, total numbers of each copepodite instar and total nauplii were translated into percentages of the whole sample population.

Temperature readings from Mazinaw and Charleston were made in 1981 with a Whitney underwater thermistor. Other

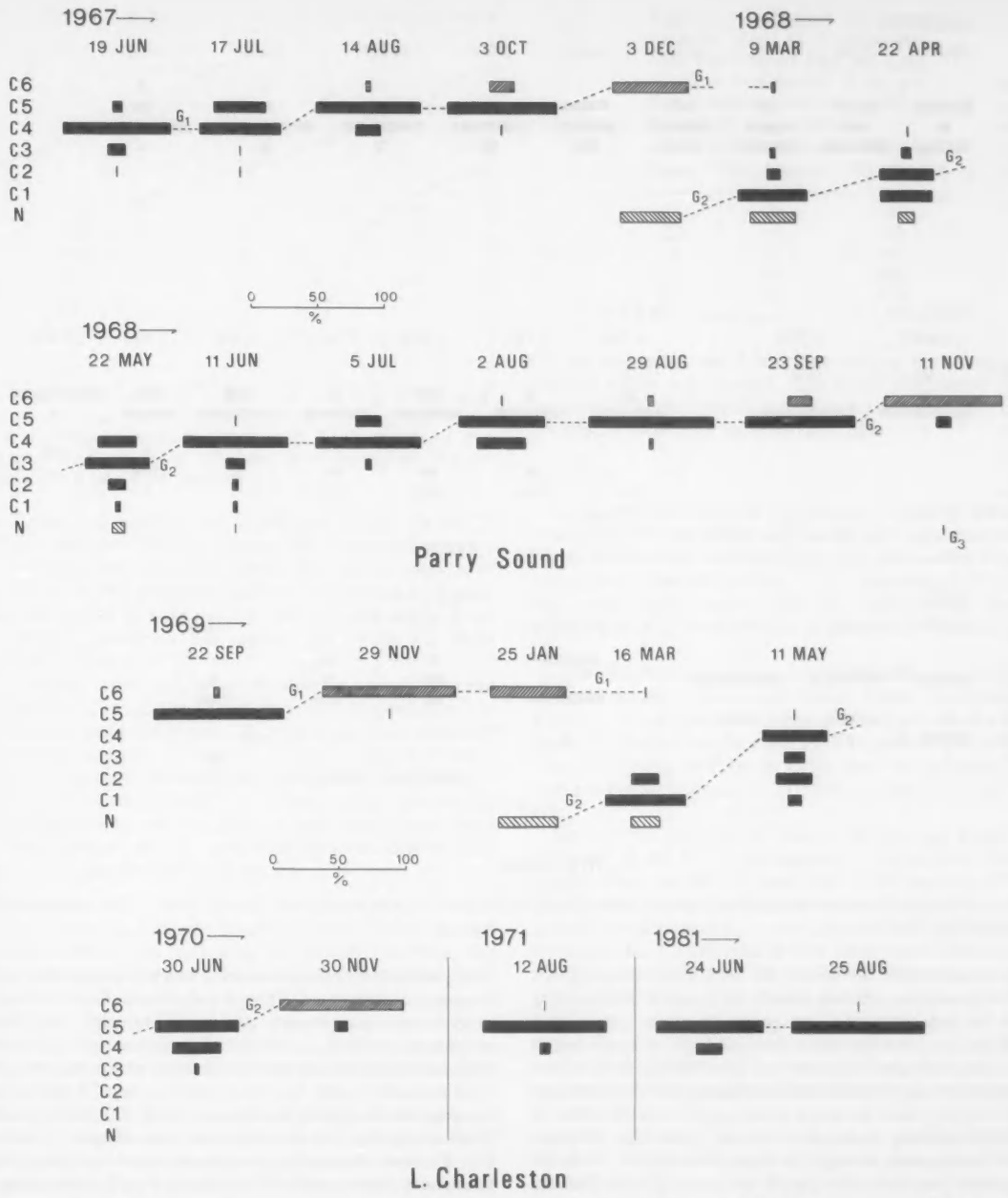

FIG. 2. Life cycles of *S. calanoides* in Parry Sound (adapted from Carter 1969) and Lake Charleston. Finely hatched bars = adults (C6); solid bars = copepodites 1–5 (C1–C5); coarsely hatched bars = nauplii (N). Broken lines indicate path of development of each generation (G).

morphometric and physical data are either from Carter (1969) and Carter's unpublished data or from Dadswell's (1974) study.

In October 1983, additional collections were made from Kettle Lake of the Gatineau set. Unfortunately only a single specimen of *S. calanoides* was found in all the samples. This area has been increasingly subject to acid rain and a critical lowering of the pH in this lake during the past 11 yr might explain the sudden decline.

Results

Life Cycles

Southern Ontario

In Parry Sound, Georgian Bay, and Lake Charleston *Senecella calanoides* has a simple univoltine life history with a single generation only developing at any time (Fig. 2). In both lakes adults appeared first in late summer but the majority of instars

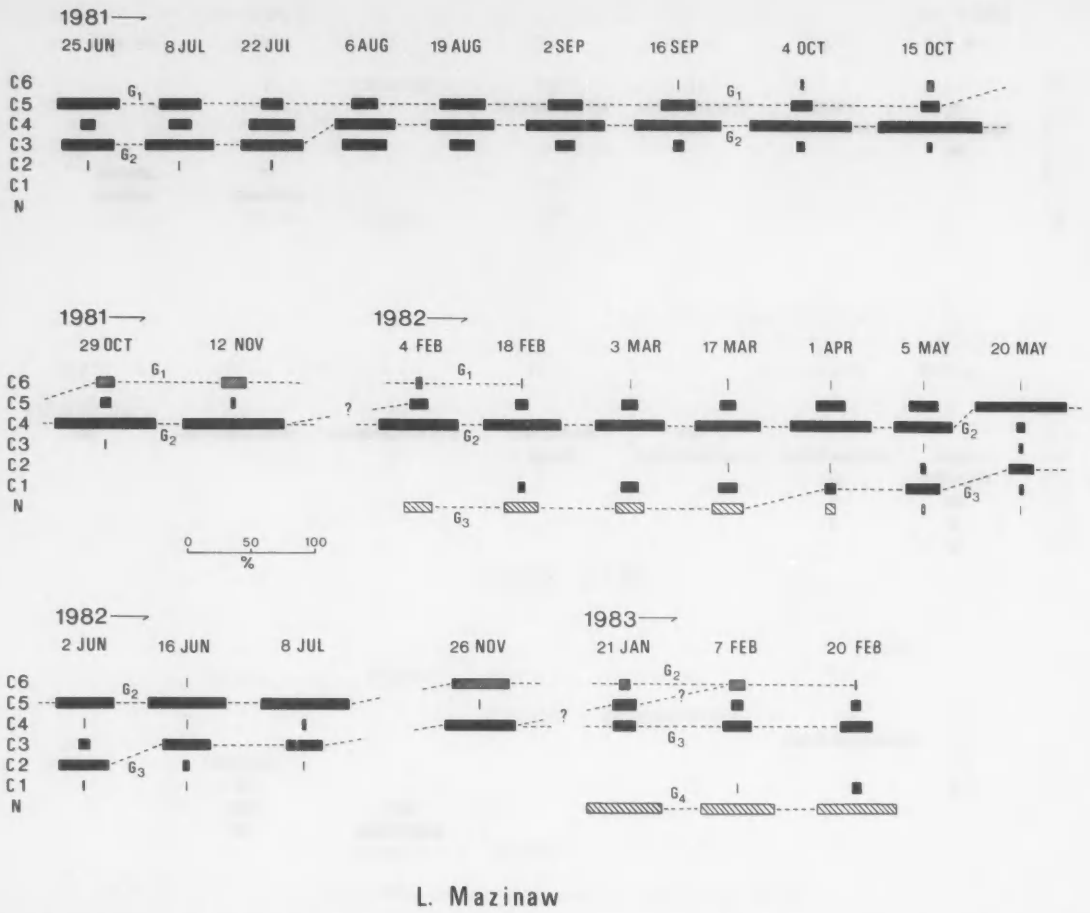

FIG. 3. Life cycle of *S. calanoides* in Lake Mazinaw. Broken lines indicate path of development of each generation (G). Instar symbols and bars are as defined in Fig. 2.

were not mature until November. Females do not carry egg sacs so it is impossible to estimate exactly the length of the spawning period, but it is apparently confined to the winter as no adults were found in either lake after March. Nauplii were present in Parry Sound between December and late May and the situation in Charleston was probably similar although development here may be slightly more advanced as no nauplii were found on 11 May 1969. During spring and summer there was slow but smooth progression through the copepodite instars, with the populations from both lakes more or less in phase. The key feature of the univoltine life cycle is a unimodal distribution of instars as soon as adults of the previous generation have disappeared. A weak bimodality occurred in Charleston on 11 May 1970 but this was probably due to sampling error as it did not appear on any other sampling date.

The life history of *S. calanoides* in Lake Mazinaw shows a radical departure from this simple univoltine model (Fig. 3). On 25 June 1981 there were two modes, at C3 and C5, which were slowly replaced during the summer by a single mode at C4. Adults appeared during the autumn, but the C4 mode persisted through 12 November and together with the adults formed a new bimodality. Winter prevented sampling until early February 1982, at which time the mode at C4 was still strong and a cohort of nauplii had appeared. Thus, it was obvious that three distinct generations were present, the remaining adults (G_1), their naupliar offspring (G_3), and the stationary animals at C4 (G_2). While a few individuals were in C5 at this time it was not until 1 April that a detectable movement from C4 into C5 commenced; this was not completed before early June. G_3 had meanwhile finished naupliar development and now formed a mode at C2. The two remaining generations continued development throughout the summer and autumn and by 26 November, G_2 was adult and G_3 at C4. By 21 January 1983, adult females of G_2 had spawned the nauplii of G_4. At this time the mode at C4 had shrunk considerably, while that at C5 had correspondingly grown, suggesting that some development may have already recommenced in the overwintering generation (G_3).

In Mazinaw, therefore, *S. calanoides* has a semivoltine (2-yr) life history with two fractions co-occurring but out of phase by 1 yr (Fig. 4). During winter, when the older generation spawns, the younger generation remains in the fourth copepodite instar before recommencing development in the spring (or earlier). Whether the more advanced individuals of any one generation are able to mature during their 1st yr is not known. Even if, as

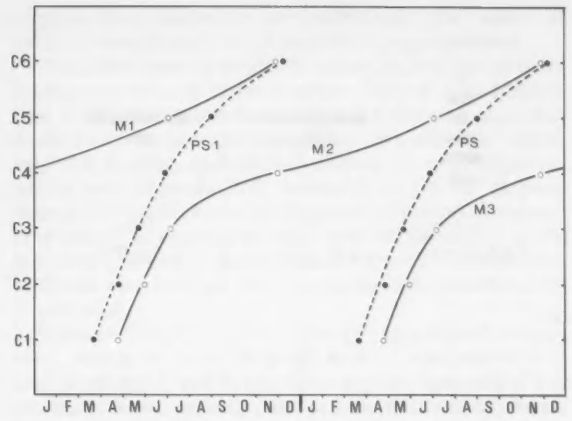

FIG. 4. Schematic instar development in *S. calanoides* of two generations in Parry Sound (PS) and three generations in Lake Mazinaw (M) during a 2-yr period.

seems probable, members of G_3 advanced from C4 to C5 between November 1982 and January 1983 there is no certainty that they progressed any further at that time. The key feature of this 2-yr life cycle is a bimodal distribution of instars at all times except the period between midsummer and midautumn when the younger generation has reached C4, while the older generation is stalled at C5.

By plotting individual instar abundances against time and applying Rigler and Cooley's (1974) method in which duration of C1 is estimated from its time–abundance curve we calculated approximate durations of instars C2 through C5 for G_2 in Parry Sound and a combination of G_2 and G_3 in Mazinaw (Table 1). While durations of each of the first three instars are roughly comparable between the two lakes, in Mazinaw C4 lasts about five times longer and C5 more than twice as long as their respective counterparts in Parry Sound.

Other regions

In 51 of the single-sample lakes the instars showed distinct unimodal distributions indicating a probable univoltine life history; of course, in those lake sampled between midsummer and midautumn a unimodal distribution would be expected regardless of type of life history (see above). In one lake, Mistassini, there was a weak bimodality, while in two others, Antoinette and Kettle, the bimodalities were strong and unmistakable (Fig. 5).

Instar distribution in Mistassini was broadly similar to that in Mazinaw during the same period (8 July 1981 and 8 July 1982; Fig. 3) although in Mistassini a much greater proportion of younger copepodites were still in C2. Despite the weakness of the bimodality, a semivoltine life history in Mistassini is further suggested by the fact that the instars at C5 (the putative older generation) were advanced far beyond those in Lakes Chibougimau, de la Surprise, la Trêve, and Baudeau, all sampled during the same general period. The sample from Lake Antoinette was from mid-October and the instars were spread throughout all copepodite stages with strong modes at C2 and C5. It seems highly unlikely that the younger instars would have been able to develop rapidly enough to mature during that winter and a semivoltine life history is strongly suggested in this lake. In the Gatineau set the bimodal instar distribution in Kettle Lake is radically different from the unimodal distributions in Lakes Cobble, Nottawissi, and Piscatosine, all four lakes having been sampled within a 3-d period. The Kettle distribution closely approximated that in Mazinaw on 2 June 1982 and a semivoltine life history is certainly indicated here also.

TABLE 1. Comparison of instar durations (days) of *S. calanoides* from Parry Sound (G_2) and Lake Mazinaw (combination of G_2 and G_3), as determined by the method of Rigler and Cooley (1974).

Instar	Parry Sound	Mazinaw
C1	28	35
C2	30	39
C3	38	45
C4	52	264
C5	78	173

Body Sizes

Cephalothorax lengths of copepodites 1–3 and of females of copepodites 4–6 in the 13 lakes of the three sets are shown in Fig. 6. While males were measured, they are omitted from this discussion for sake of brevity: in all cases males of C4 and C5 were very slightly smaller than the corresponding females, while males of C6 were always slightly smaller than males of C5.

In the southern Ontario set, length differences in C1 and C2 between the three lakes were minor. From C3 through C6, however, it is obvious that all instars from Lake Mazinaw were markedly smaller than the same instars in either Parry Sound or Lake Charleston and by amounts that far exceeded those between the same instars of different generations in the same lake.

For the two lake sets in Quebec the data are incomplete. However, in the Abitibi set Antoinette instars were distinctly smaller than those from Chibougimau, de la Surprise, la Trêve, and Baudeau. A trend toward smaller size can also be seen in the later instars of Mistassini. In the Gatineau set Kettle instars are the smallest at C2 and smaller than those from Nottawissi and Piscatosine at C3. At C4 the two Kettle specimens were both smaller than those from Cobble and Piscatosine. At C5 the Kettle instars were extremely small, more so than those from any of the other 12 lakes, and of equal size or smaller than C4 instars from Coble and Piscatosine. Clearly there is a strong trend toward increasingly smaller size with age in copepodites in Lake Kettle.

In the remaining 44 lakes where *S. calanoides* showed unimodal distributions cephalothorax lengths of later copepodites (C4–C6) in every instance were greater than in the corresponding instars in Mazinaw, Antoinette, Mistassini, and Kettle.

Discussion

Presumably, winter breeding and spawning is obligatory in *S. calanoides* and if development during the 1st yr of life is retarded for whatever reason then durations of the later pre-adult copepodites will be greatly lengthened and maturation postponed until the end of the 2nd yr. While there is no absolute certainty that the 2-yr life cycle is not genetically fixed in populations where it occurs, the behaviour of G_3 in Mazinaw

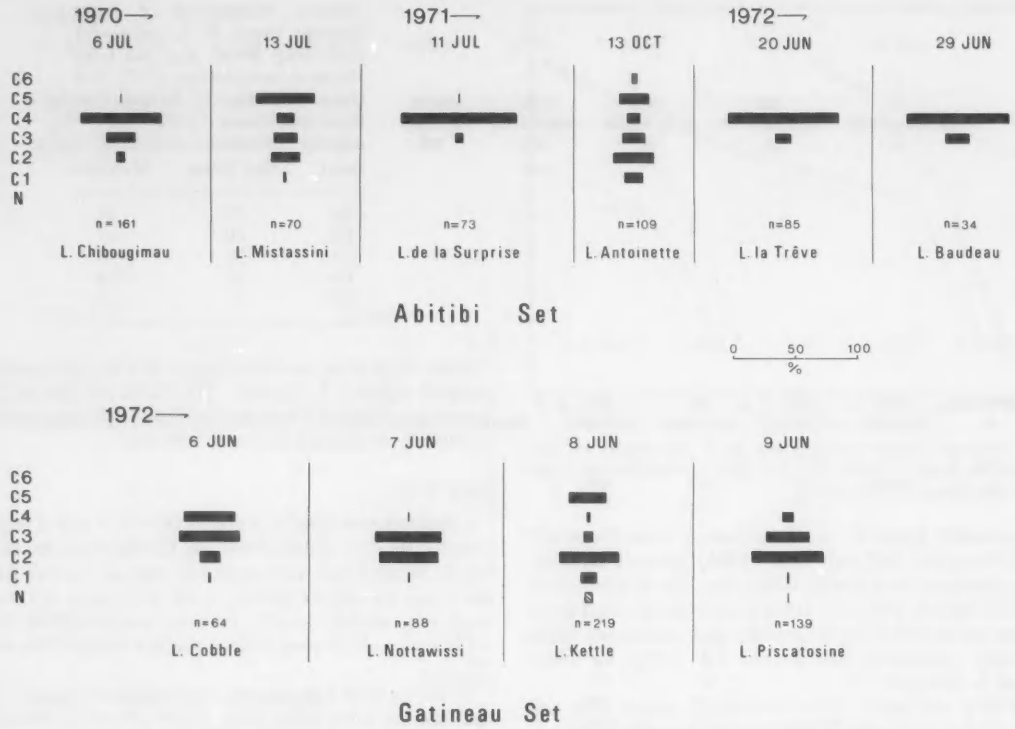

FIG. 5. Instar distributions of *S. calanoides* from single dates in lakes of the Abitibi and Gatineau sets.

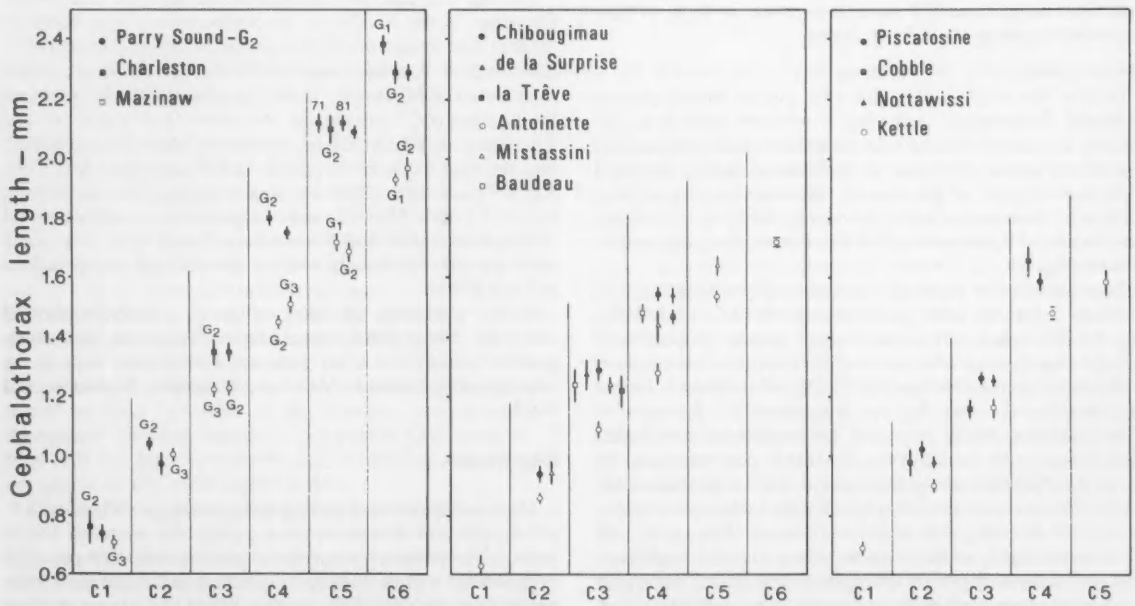

FIG. 6. Cephalothorax lengths of C1–C3 and females of C4–C6 of *S. calanoides* in the 13 lakes. Values are means and 99% C.I. Horizontal bars indicate ranges in two instances where $n = 2$.

suggests that changes in the environment (the winter of 1982–83 was unusually mild) may affect instar durations.

The method through which *S. calanoides* doubles its development period in Mazinaw is curious. Most of the additional time is spent in C4 but the duration of C5 is also more than doubled and the younger copepodites may also live slightly longer. It is highly questionable whether the term "diapause" applies here. Elgmork (1980) referred to an "active" diapause amongst cyclopoids where development and growth are arrested in a particular copepodite instar with no dormancy in the sediments. However, this operation requires a descent into profundal waters and we have no evidence that this occurs with *S. calanoides*.

Miller et al. (1977) have suggested that isochronal development, such as occurs in the genus *Acartia*, is an adaptation to limit durations of later instars where they are vulnerable to fish predation. *Senecella calanoides* in Lake Mazinaw has highly nonisochronal development and this could be evidence that in this lake at least its susceptibility to predation is either very low or nonexistent.

Senecella calanoides is the only freshwater calanoid copepod in the world that may require 2 yr for development (Allan and Goulden 1980) although this has been found in marine calanoids at the highest latitudes (Cairns 1967). In freshwater cyclopoids 2-yr and even 3-yr life cycles have been reported (Elgmork 1965; Halvorsen and Elgmork 1976) but these always require a period of diapause in the sediment.

Many studies on natural and laboratory populations of marine and freshwater copepods have shown that development rates are directly, and instar durations inversely, related to temperature (McLaren 1965; Geiling and Campbell 1972). There is evidence that food also may be important. Weglenska (1971) found that postembryonic development time in *Diaptomus graciloides* was inversely related to nutrition. McLaren (1963) agreed on the importance of food but argued that it has a stop–go effect: below a certain nutrition threshold development ceases entirely, while above this level development rates are independent of food.

The relative importance of temperature and food in natural populations is usually difficult, or even impossible, to assess. For instance, does an arctic lake population of a particular species develop more slowly than one in a temperate lake because waters are colder in high latitudes, or because annual phytoplankton production is lower, or are both factors involved? *Limnocalanus macrurus* in Parry Sound takes about 6 mo to develop (Carter 1969) whereas in Char Lake in the high arctic it requires about 9 mo (Roff and Carter 1972). The problem is even more vexing when considering developmental differences among populations in lakes at the same latitude because lakes that are deep and have a large volume of cold water are precisely those lake that would be expected to be low in nutrients and hence food-poor.

We have evidence that the 2-yr life cycle of *S. calanoides*, which occurs in at least 1 and possibly 3 more of the 13 lakes, may be both temperature and food related (see Table 2). Each of the four lakes has a strong hypolimnetic component. Mazinaw has great maximum and great mean depth. It is long and narrow with only a short fetch across which the prevailing westerly winds can generate energy to drive heat downward, depress the thermocline, and thicken the epilimnion. Parry Sound is also very deep but almost circular and is noted for its periodic rough seas. Mistassini is one of the deepest lakes in eastern Canada although its mean depth has not yet been calculated. Antoinette is fairly shallow but has a small area and is sheltered from the winds by steeply rising land behind its western and northwestern shores. Moreover, its northern location insures a relatively short heating season. Kettle is only moderately deep but with a relatively great mean depth. It has a very small area and is also protected by high land to the west. That these morphometric and geographic features are instrumental in maintaining somewhat cooler waters in Mazinaw, Mistassini, and Kettle is indicated in available temperature curves (Fig. 7). Transparent waters are usually associated with oligotrophy and low phytoplankton productivity. Mazinaw, Mistassini, Antoinette, and Kettle have Secchi depth readings that in all but a single instance are higher than in the other lakes of their sets (Table 2), suggesting that food in these lakes may be limited.

TABLE 2. Morphometric and physical data for the 13 lakes. Semivoltine lakes are indicated with an asterisk.

Lake	Z_{max} (m)	Z_{mean} (m)	Area (ha)	Secchi depth (m)
S. Ontario set				
Parry Sound	112	33	8 000	3.2
Charleston	92	17	1 700	3.7
Mazinaw*	135	41	1 570	6.0
Abitibi set				
Chibougimau	56	11	17 650	5.4
Mistassini*	184	—	100 000	9.0
de la Surprise	27	12	4 965	2.8
Antoinette*	27	16	115	4.8
la Trêve	15	7	4 825	3.3
Baudeau	27	—	1 825	3.9
Gatineau set				
Cobble	21	11	71	3.5
Nottawissi	36	18	1 255	4.2
Kettle*	57	35	60	6.9
Piscatosine	50	15	2 005	3.6

A large, cold hypolimnion would be important in reducing development rates only insofar as the instars remain in it most of the time. *Senecella calanoides* is a noted diel migrator (Wells 1960) and tends to occupy the upper waters at night. However, if the epilimnion is shallow, as we have postulated for Mazinaw, Antoinette, and Kettle, then the instars may never ascend high enough to experience a major temperature increase. It is also certain that its migration pattern is not the same in each lake. As part of another study at the University of Waterloo we have discovered that in Charleston *S. calanoides* C4 and C5 are close to the bottom during the day and in the upper metalimnion and lower epilimnion at night. In Mazinaw the same two instars spend the day at mid-depth and then move into the lower metalimnion at night. Both studies were conducted in August 1981. In Mazinaw and elsewhere it may be unnecessary for *S. calanoides* to penetrate the warm upper waters to find food. Fee (1976) has demonstrated that peaks of oligophotic phytoplankton species are not uncommon in and below the thermocline in clear, stratified water bodies.

It is generally accepted that McLaren's (1963, 1965) hypothesis regarding the inverse relationship between body size and developmental temperatures in marine copepods applies to freshwater species also. With multivoltine diaptomids it has been noted that the smallest generation is invariably the one that develops in the warm waters of midsummer (Comita 1972; Lai 1977; Herzig et al. 1980). Yet we have just shown that the long developmental period of *S. calanoides* in those very lakes

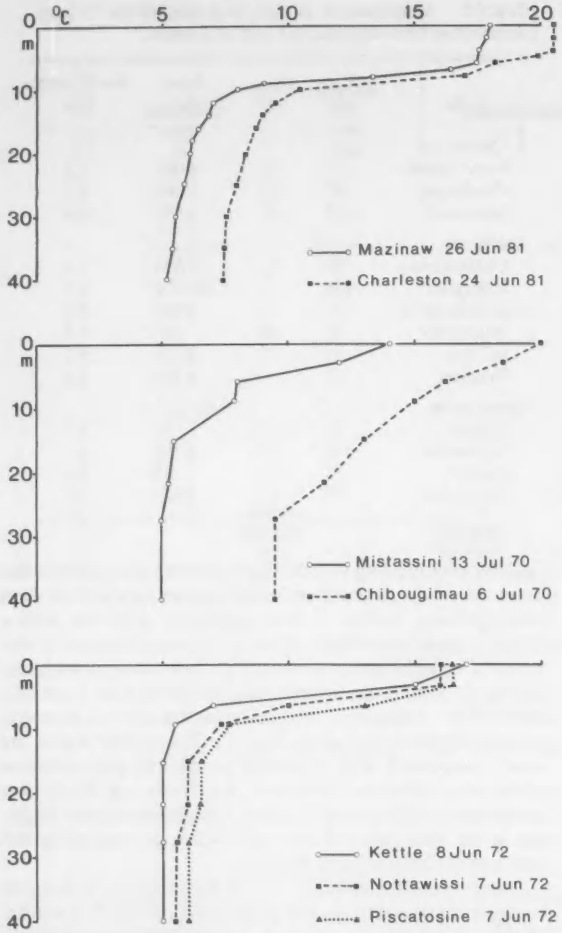

FIG. 7. Temperature curves (0–40 m) in seven lakes of the three sets.

where late copepodites are small is probably related to low temperatures. Moreover, there is no evidence that in these four lakes *S. calanoides* instars at any time experience higher temperatures than their counterparts in the other lakes of their respective sets. Therefore, the assumption that small body size in 2-yr *S. calanoides* is related to temperature must be rejected.

The relationship between body size and nutrition is still disputed. Weglenska (1971) successfully cultured larger copepodites of *D. graciloides* by increasing food rations. In laboratory experiments Elmore (1983) discovered a strong positive relationship between food and metasome length in three *Diaptomus* species. Neill (1981) noted that two species of *Diaptomus* showed decreases in body length under lowered food levels in enclosures. However, Elgmork and Halvorsen (1976) found that size differences in two populations of *Cyclops strenuus* were independent of quantity and quality of food. With marine copepods there is also some evidence indicating that quantity of food has a positive effect on body length of at least some species (Deevey 1960; Frost 1974). Vidal (1980) found that the effect of food concentration on size of *Calanus pacificus* and *Pseudocalanus* sp. became more pronounced with increasing stage of development. Vidal's standard of measurement was body weight rather than length, so his results should be treated with caution. Nevertheless, his findings accord with ours for it was instars C4–C6 of *S. calanoides* where body length differences became most striking. Moreover, Vidal showed that the critical food concentration for growth is higher for a large species than a small one, which also suggests that size in *S. calanoides* may be controlled by food. However, as all our evidence relating to primary production in the lakes is indirect, this line of speculation should be pursued no further. Nevertheless, it is noteworthy that an analogous situation occurs within the Mysidacea. Both growth and developmental rates of *Mysis relicta*, another glacial relict, differ greatly between North American environments with productivity indicated as the major controlling factor (Lasenby and Langford 1972; Morgan 1980, 1981).

The implication of a semivoltine life history for secondary production is difficult to assess. Assuming that different instars do not compete for the same food items, the numerical abundance at any time should theoretically be twice that if one generation only were present. On the other hand, this gain in abundance ultimately must be cancelled out by the doubling of development time. The population in Mazinaw was much greater than we have encountered in any lake with either life cycle ($>10\,000 \cdot m^{-2}$ on about half the sampling dates), roughly triple that in Parry Sound (Carter 1969). We hope to undertake further studies on *S. calanoides* in Mazinaw to clarify the mechanism controlling development time and to determine production rates.

Acknowledgments

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Three-Dimensional Prey Reaction Field of the Juvenile Coho Salmon (*Oncorhynchus kisutch*)

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Dunbrack, R. L., and L. M. Dill. 1984. Three-dimensional prey reaction field of the juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 41: 1176–1182.

Filmed observations of the feeding behaviour of juvenile coho salmon (*Oncorhynchus kisutch*) cruising in a large aquarium were used to determine the three-dimensional shape of their reaction field, and to estimate the cross-sectional area of the effective volume searched for prey (scanning area). Reaction distance was greatest above the horizontal visual plane and ahead of the transverse visual plane, and this corresponds to the feeding behaviour of fish observed in the wild. The scanning area for a given size of prey was obtained by plotting all captures as projections on the transverse plane. This distribution of points was then divided into a series of concentric bands characterized by prey attack probabilities, which were then used as weighting factors in the final calculation of the scanning area. Our results and techniques are discussed in relation to previous studies of fish reaction fields, and a simple method of estimating scanning area for salmonids is suggested.

On a utilisé des observations filmées du comportement alimentaire de saumons cohos (*Oncorhynchus kisutch*) juvéniles se déplaçant dans de grands aquaria pour déterminer la forme tridimensionnelle de leur champ de réaction et pour évaluer l'aire transversale du volume réel parcouru à la recherche de proies (aire d'exploration). La distance réactionnelle était plus élevée au-dessus du plan visuel horizontal et en avant du plan visuel transversal; cela correspond au comportement alimentaire observé chez les saumons sauvages. On a calculé l'aire d'exploration pour une taille donnée d'une proie en portant sur un graphique toutes les captures comme projections sur le plan transversal. Cette distribution des points a ensuite été divisée en une série de bandes concentriques caractérisées par les probabilités d'attaque des proies, probabilités qui servirent ensuite comme facteurs de pondération dans le calcul final de l'aire d'exploration. On présente les résultats et techniques en fonction des études antérieures sur les champs de réaction du poisson et on élabore une méthode simple pour l'estimation de l'aire explorée par les salmonidés.

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Selective feeding on large prey by predatory fish has been related to the greater visibility of larger prey items (Brooks and Dodson 1965; Ware 1972, 1973; Werner and Hall 1974; Confer and Blades 1975; Moore and Moore 1976; Wańkowski 1979, 1981; Dunbrack and Dill 1983). Models incorporating a positive relationship between prey size and the distance at which prey will be detected and attacked (reaction distance) have shown good agreement between predicted and actual dietary size-class frequencies (Ware 1973; Werner and Hall 1974; O'Brien et al. 1976; Eggers 1977; Gibson 1980; Dunbrack and Dill 1983). In the construction of such models it is often sufficient to specify only the relative reaction distance (RD) to various sizes of prey, but if quantitative diet predictions are required, or if the feeding space is constrained, actual RDs and the shape of the reaction field (the visual field surrounding the fish) must also be included (Confer et al. 1978). The relationship between prey size and frontal RD has been obtained for several fish species, but relatively less work has been done on the shape of reaction fields and how this may affect the prey encounter process.

As a cruising fish moves through the water column, it searches a somewhat cylindrical volume whose longitudinal axis is the fish's trajectory. For such a predator, the rate at which it encounters prey will be directly proportional to the effective cross-sectional area of this search volume, which we term "scanning area." Confer et al. (1978), in their study of the reaction field of cruising lake trout (*Salvelinus namaycush*), approximated the dimensions of this cross section using the means of observed RDs to prey attacked adjacent to the transverse plane (the plane perpendicular to the fish's longitudinal body axis and passing through both eyes). Luecke and O'Brien (1981) described the reaction field of stationary bluegill sunfish (*Lepomis macrochirus*) in terms of 0.95 and 0.05 detection probability contours for a number of visual planes, including the transverse one. The reaction field map they constructed provides a useful model of prey encounter for a fish such as the bluegill, which tends to pause after each capture and search for the next prey item from a stationary position (Luecke and O'Brien 1981), but it is not entirely appropriate for a cruising predator, which may perceive its prey somewhat differently. For example, the movement of a cruising predator could affect the detectability of prey items by altering their apparent motion, or the length of time they are present in the predator's reaction field. More importantly, the technique of

dividing the reaction field into discrete visual planes, used by both Confer et al. (1978) and Luecke and O'Brien (1981), while convenient from a descriptive point of view, leads to an estimate of the scanning area that is based only on attacks made adjacent to the transverse plane. Not only does this ignore the role that the remainder of the reaction field plays in prey detection, but it is likely to result in a biased estimate of the scanning area. This bias stems from the fact that attacks directed in or close to the transverse plane represent only a small portion of all attacks, most of which are directed ahead of this plane. The probability that a prey item will be detected as a function of its distance from the fish's search trajectory, necessary information for an unbiased estimate of the volume searched, is not explicitly contained in such mean RDs and can only be obtained by examining the role of the entire reaction field in prey detection.

In the work described here, an attempt is made to identify this bias and provide a description of the scanning area based on the entire reaction field. To facilitate comparison of the results of this study with those of Confer et al. (1978) and Luecke and O'Brien (1981), a reaction field map is also constructed.

Methods

Experimental Procedure

The experimental apparatus consisted of a plywood tank 70 × 70 × 90 cm (length × width × depth). The inside of the tank was coated with white nontoxic epoxy paint, and the bottom and sides were marked off in a 5 × 5 cm grid of black lines. Lighting was provided by four 75-W flood lights, which gave a surface illumination of approximately 600 lx. Two video cameras suspended 130 cm above the water surface provided paired video records of feeding bouts for stereo analysis.

Prey items (*Daphnia pulex*, mean width 1.26 ± 0.14 (SD) mm) were introduced to the tank via two horizontal and diagonally opposed pipes situated at a depth of 35 cm, through which water taken from the tank outlet was circulated back to the tank by a centrifugal pump. This technique of prey introduction produced a relatively even distribution of *Daphnia* from top to bottom, as no significant difference in *Daphnia* density was found in a comparison of eight "top" (400-mL cylindrical sampler centered at 17.5 cm depth) and eight "bottom" (centered at 52.5 cm) samples taken within 3 min of the introduction of 1000 *Daphnia* to the tank.

The five juvenile coho salmon (*Oncorhynchus kisutch*) used in the experiments (Table 1) were seined from the Salmon River, Langley, B.C., and maintained in the laboratory in individual aquaria. A single fish was placed in the tank 2 d prior to the beginning of recorded feeding bouts and on the day following introduction was fed as during recorded bouts to familiarize it with the feeding regime. To initiate a feeding bout, 10 *Daphnia* were introduced to the tank via the pipes and the pump was turned off. During the subsequent feeding period, an observer above the tank activated a light whenever a capture was made. The light was not visible to the fish but appeared on both video records and thus served to synchronize the two recordings and to allow discrimination (and deletion) of attacks made on nonfood items. To minimize the effect on RD of the initial movement imparted to the prey by the pump, captures made within 20 s of pump stoppage were ignored. Also ignored were captures made within 5 s of a previous capture, the intent being to eliminate short RDs to prey fortuitously encountered adjacent to a prior capture. A total of 12 feeding bouts were filmed between 9 a.m. and 12 noon on each day experiments were run.

TABLE 1. Body length and number of attack sequences analyzed for each of the five fish used in the experiment.

Fish	Fork length (mm)	Attacks analyzed
1	55	76
2	50	70
3	54	71
4	58.5	84
5	56	4
		$\Sigma = 305$

During an attack sequence, the fish initially oriented its body axis in the direction of the intended prey item. This was followed by a rapid acceleration from cruising velocity (which averaged 8.1 ± 0.56 (SE) $cm \cdot s^{-1}$) in a straight line towards the prey. Prey capture was typically followed by deceleration and body rotation away from the attack trajectory. Attack parameters were defined as follows (see Fig. 1): reaction distance (RD) is the snout-to-snout distance between fish positions just prior to orientation and at capture; attack bearing (β) is the angle in the horizontal plane between the body axis prior to orientation and the attack trajectory; attack elevation (ϵ) is the angle between the attack trajectory and the horizontal plane (the search trajectory is assumed to be horizontal). Thus defined, RD is not necessarily equivalent to sighting distance. It is possible that prey are sighted at one distance but not attacked until this distance has been reduced to some threshold that may be subject to behavioural modification (Dunbrack and Dill 1983).

3-D Analysis

For each attack sequence, the paired video records were used to obtain the coordinates (x, y, z) of three points: the fish's head and tail just prior to orientation to the prey and the fish's head at the point of capture. This was done for a total of 305 attack sequences distributed among five fish (Table 1). The paired head and tail positions provide an estimate of the fish's search trajectory necessary to calculate attack bearing. The details of the technique used for 3-D analysis and estimation of attack parameters are described in Dunbrack (1984), along with simulations to determine the accuracy of the method.

Reaction Field Map

The coho reaction field was mapped in three planes: transverse (through the eyes), horizontal (along the mid-body line), and sagittal. Each of these was in turn taken as forming the equatorial plane of a sphere (attack initiation at the center) and an attack was included in a particular plane if the capture occurred within ±30° latitude of it. Each of these planar belts was further divided into eight equal sectors, which thus measured 60 × 45° (Fig. 2).

Scanning Area

All prey items captured above and ahead of the fish were plotted as projections on the transverse plane with their distance from the origin being equal to their perpendicular distance from the search trajectory. This distribution of points was divided into a series of concentric bands characterized by attack probabilities that, assuming that prey were evenly distributed throughout the water column, can be estimated from the relative density of attacks within each band. A weighted cross-sectional

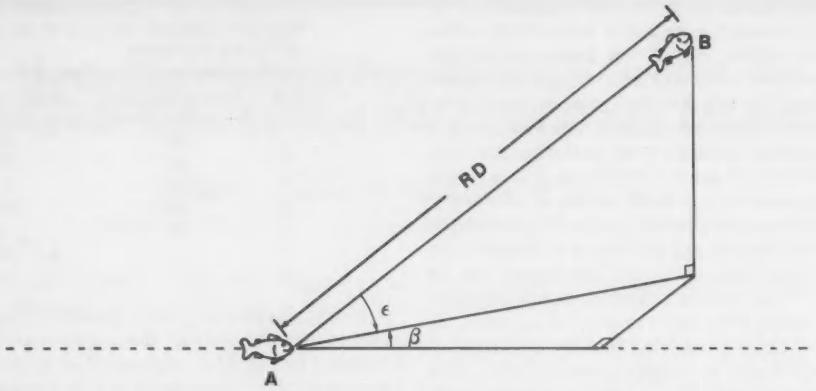

FIG. 1. Geometry of the attack parameters. A, position of the fish just prior to attack initiation; B, position at point of prey capture; β, attack bearing measured in the horizontal plane; ϵ, attack elevation between the horizontal plane and the attack trajectory; RD, reaction distance.

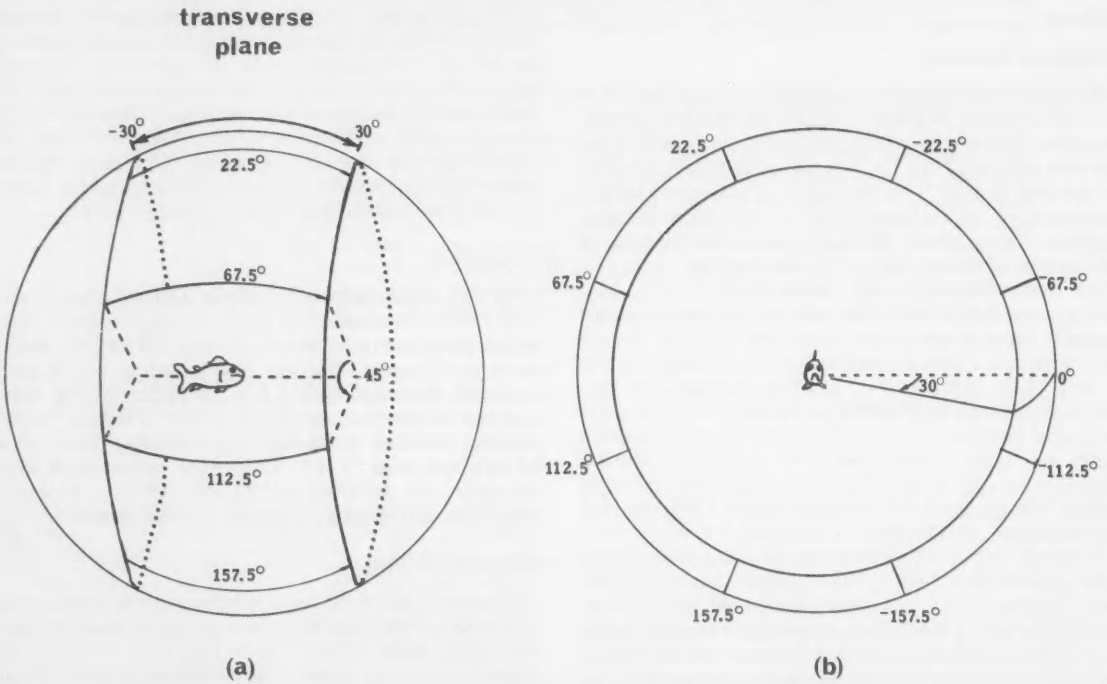

FIG. 2. Lateral (a) and frontal (b) views of the visual sectors comprising the transverse plane. In this case the transverse plane is the equatorial plane and the sectors lie between ±30° latitude. Lines of longitude are 45° apart so that each sector is 60 × 45°.

area of the search volume can then be obtained by multiplying the area of each attack probability category by its corresponding attack probability and summing over all categories. This is the scanning area.

Results

Reaction Field Map

Values of attack bearing (longitude) and elevation (latitude) for each of the 305 sequences analyzed are shown in Fig. 3. This figure contains no information on RD. The data are plotted in polar coordinates in Fig. 4 to show the relationship between RD and angular orientation for each of the three attack planes. There is a tendency for RD to increase with increasing elevation. This trend is significant for both the sagittal (ANOVA $F_{4,69} = 6.1$, $p < 0.001$) and transverse ($F_{4,163} = 6.3$, $p < 0.001$) planes. In the sagittal plane (Fig. 4a) the maximum mean RD is directly above the fish and the minimum is directly below. In the transverse plane (Fig. 4c) the minimum mean RD is still directly below the fish, but the maximum mean RD is now in the 22.5–67.5° sector. Although RD appears to increase laterally in

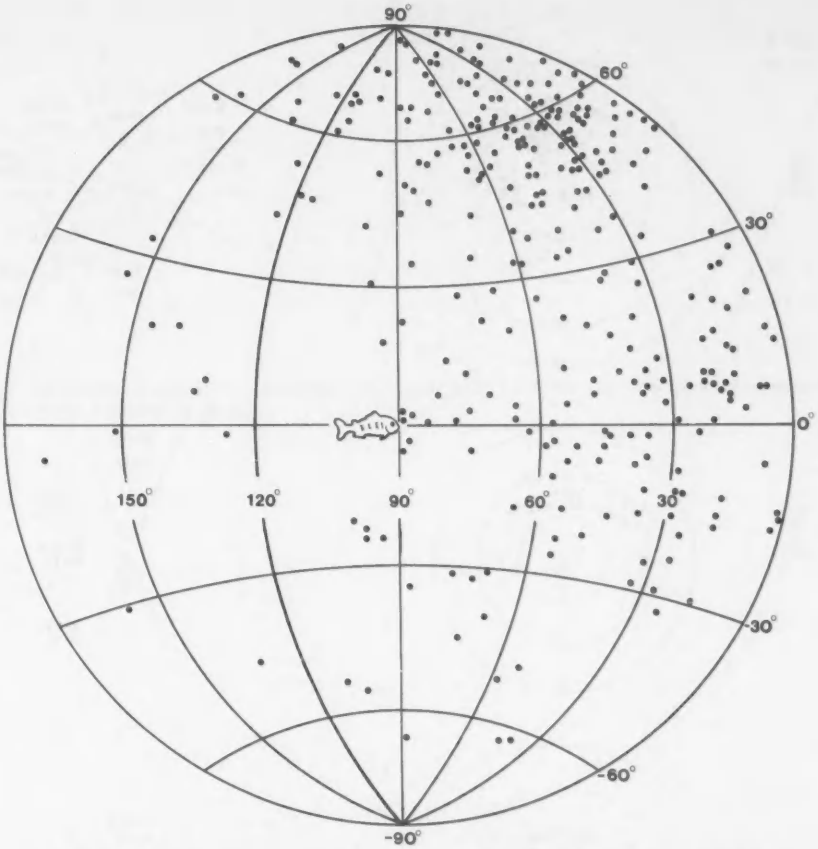

FIG. 3. Bearing (β, longitude) and elevation (ε, latitude) of the 305 attacks analyzed. The fish's left hemisphere has been reflected upon the right hemisphere.

the horizontal plane (Fig. 4b), this trend is not significant ($F_{2,110} = 0.4$).

The pattern of attacks observed in a study such as this will be affected to a certain extent by the size of the apparatus relative to the potential reaction field of the fish. If the apparatus is too small, much of the reaction field will be truncated and observed RDs will be shorter than in a larger tank. To investigate the effect that truncation of the reaction field may have had on the results, the data were reexamined after all attacks made towards and within 30 cm of a wall, the surface, or the bottom were eliminated. It was felt this procedure would rectify most truncation problems, as less than 5% of all RDs were greater than 30 cm. The only substantial changes occurred in the lateral sectors of the horizontal and transverse planes, where mean RDs increased 23 and 17.2%, respectively (Fig. 5). Using this correction, RD in the horizontal plane was now significantly greater laterally than frontally ($F_{2,78} = 3.9$, $p < 0.05$).

Scanning Area

All attacks above the horizontal plane and not expected to have been affected by truncation (see above) were plotted as projections on the transverse plane. Concentric lines were drawn around areas of approximately equal attack density (Fig. 6) and the attack probability for prey within each band calculated as D_j/D_{max}, where D_{max} is the attack density in the band closest to the attack trajectory and D_j is the attack density in band j. The weighted estimate of that portion of the scanning area above the horizontal plane obtained using this technique (i.e. $\Sigma_j(\text{AREA}_j)(D_j/D_{max}) = 932\,\text{cm}^2$) was 1.2 times that found using only mean RDs in the transverse plane (776 cm^2). A good estimate of the scanning area below the horizontal plane could not be obtained using this procedure because of the low number of attacks recorded there.

Discussion

Specific visual adaptations should develop in response to a variety of selection pressures. For a visual predator a significant component of this selection will be related to foraging activities, and we would therefore expect directional prey detection ability to be correlated with mode of foraging. Coho salmon feed while holding a station in running water or actively searching in still water and, like most predators, encounter prey primarily in the forward directed hemisphere. In the field, because of their generally low position in the water column and the presence of much surface food, more of their attacks are directed above than below the horizontal plane (K. J. Puckett, Dep. of Biosciences, Simon Fraser University, pers. comm.). The relatively large

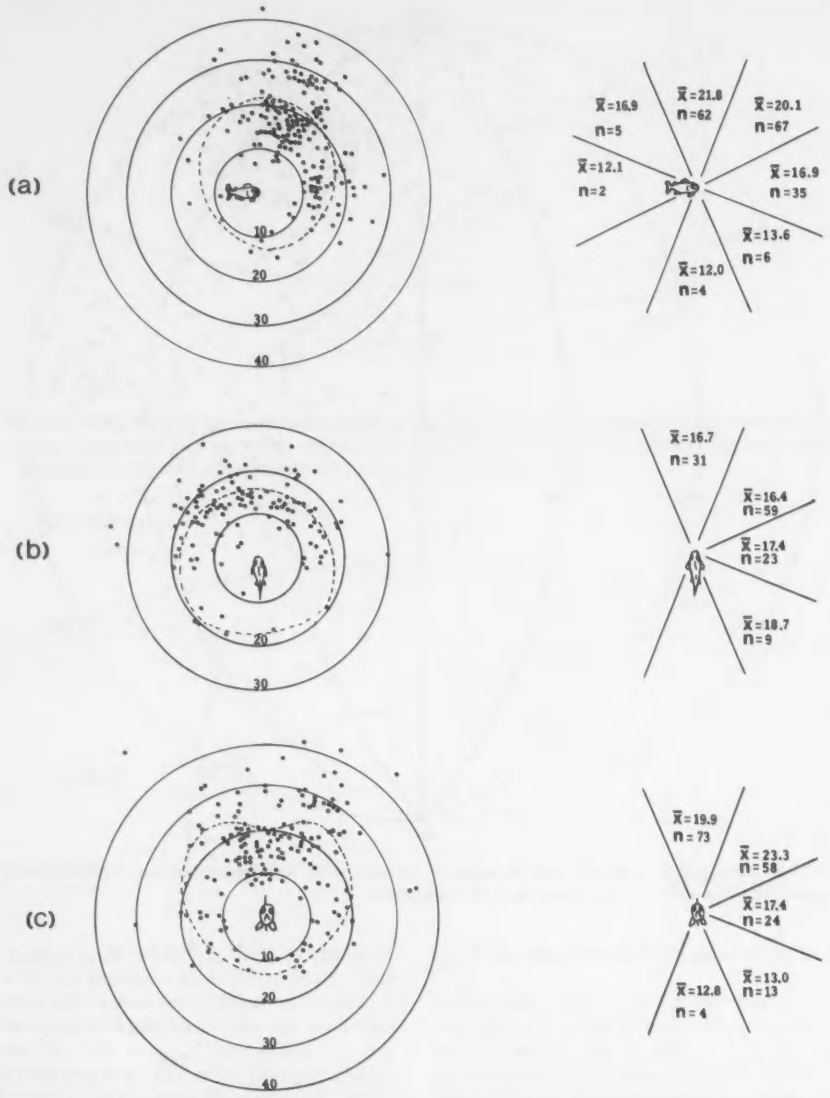

FIG. 4. Left: attacks plotted on polar coordinates for sagittal (a), horizontal (b), and transverse (c) visual "planes". Concentric circles represent distances from the fish's snout (cm). Broken lines are drawn through the mean RD value for each sector. Right: mean RD ($\bar{x}$) and number of attacks (n) observed for each sector of each visual "plane". Equivalent right- and left-hand (fish's) sectors are pooled.

RDs ahead and above observed in this study are thus generally consistent with coho foraging behaviour under natural conditions.

The detailed shape of the reaction field can reflect a number of proximal factors, not all of which are entirely related to vision and none of which can be easily partitioned as to effect. For example, within that portion of the visual field ahead and above, RD was greatest adjacent to the transverse plane (Fig. 4a). This could reflect corresponding patterns of visual acuity and sensitivity, but could also be related to the skewed distribution of prey encountered there (resulting from the fact that prey close to the search trajectory will normally be attacked before they reach the transverse plane), or to the increasing apparent rate of prey movement, which may enhance visibility, as prey are approached by the cruising fish.

The potential influence of the mode of foraging on the observed reaction field means that the results of various studies must be compared with caution. Confer et al. (1978) measured the attack field of lake trout searching for food while swimming in a glass aquarium. Their methodology was quite similar to ours and the two studies should therefore be directly comparable. If the probable effect of attack field truncation in their study is taken into account, the results are quite similar. This may reflect the fishes' phylogeny, similarities in the way

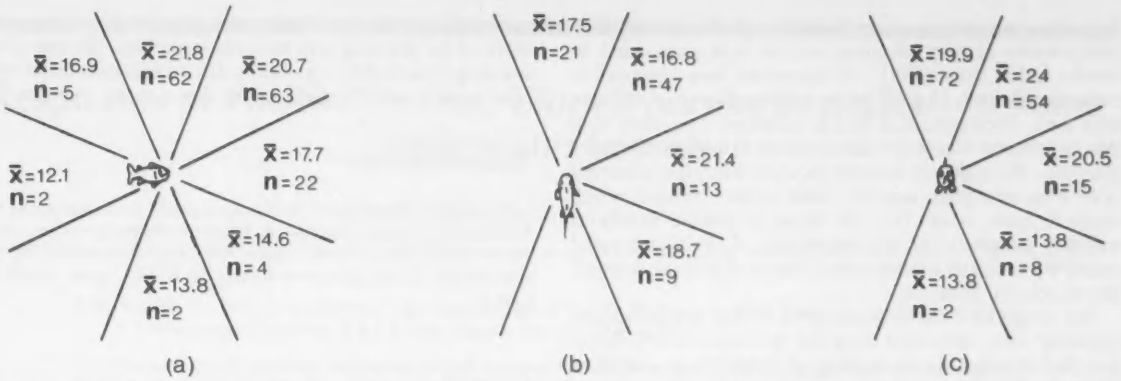

FIG. 5. Mean RD ($\bar{x}$) and number of attacks (n) observed for each visual "plane", after the data were corrected for potential truncation of the reaction field (see text and Fig. 4 caption for details).

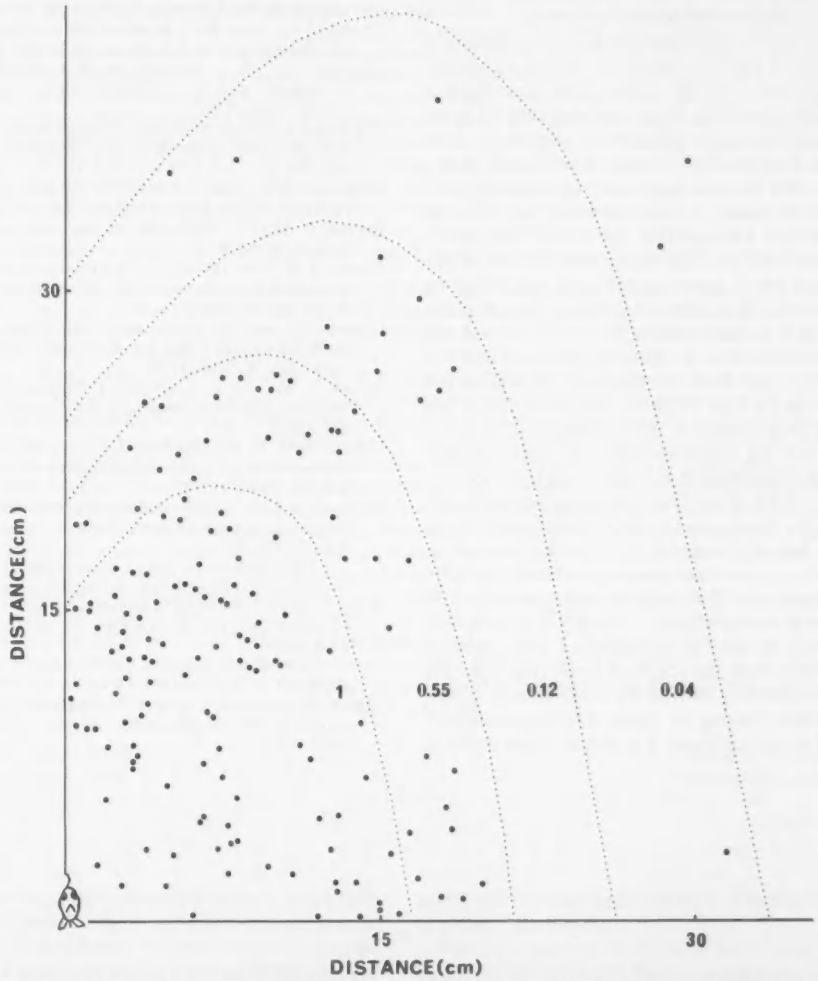

FIG. 6. Plot of all attacks not expected to have been influenced by truncation (see text), projected on the transverse plane. X- and Y-axes are perpendicular distances from the fish's search trajectory. The shape of the concentric curves was obtained by visual inspection and conforms generally to the RD data (Fig. 5c). Numbers represent the relative probability of attacking prey falling within the corresponding concentric band (D_j/D_{max}; see text).

they encounter prey, or both. Although the probabilistic interpretation of prey encounter we use here owes much to Luecke and O'Brien (1981), the procedure they employed in evaluating the prey location ability of bluegill is quite different from ours. They presented prey to stationary fish; there were thus no apparent movement cues available to the fish to aid prey detection. The relatively low prey location ability they observed in the transverse plane may be related to this technique, which seems to stress acuity (i.e. the ability to resolve an object) and may underestimate the importance of peripheral visual sensitivity to real or apparent prey movement in more dynamic prey encounter situations.

The weighted cross-sectional area of the search volume (scanning area) calculated using our technique is 20% larger than that obtained by the method of Confer et al. (1978), a difference that at low prey densities would be directly translated into a similar increase in predicted feeding rate. A change of this magnitude could be significant in modelling fish production or the impact of predation in low-productivity habitats.

An obvious drawback of our technique is its time consuming nature. Examination of the data, however, suggests a simpler estimate. It has been shown that the portion of the scanning area above the horizontal plane (Fig. 6) is approximately 1.2 times larger than the equivalent area obtained by drawing a curve through the mean RDs of Fig. 5 (transverse plane). If this relationship also holds for that portion of the scanning area below the horizontal plane, a total scanning area can be calculated. If it is then assumed that the volume searched is cylindrical, the search radius (R) giving an area of identical size to this total scanning area is approximately 20% larger than the RD in the forward sector of the horizontal plane in our large tank (frontal RD), i.e. $R \approx 1.2$RD. Confer et al. (1978) found that the frontal RD of lake trout in a narrow aquarium (RDn) was approximately 30% larger than that observed when their fish were cruising in a larger tank (RDn $\approx$ 1.3RD). Some of this difference, which they related to the increased difficulty of locating prey in any particular direction as search volume expands, is probably attributable to reaction field truncation. Correction for this effect in our study increased frontal RD by 5%. A slightly larger correction (5–10%) should apply to the "large" aquarium data of Confer et al. (1978) because of the considerably smaller size of their aquarium. Therefore, RDn may actually be closer to 1.2RD, and thus may approximate R. This suggests that a measurement of frontal RD, which is readily obtained, can be used as the radius of a hypothetical circular area approximating the scanning area. Although this approximation is empirically derived for coho salmon, it may prove useful for other cruising or stream dwelling salmonids with reaction fields of similar shape. It would be of less utility in very shallow water (such as in many streams) where the actual shape of the scanning area becomes important. The use of the scanning area model in predicting diet composition under such conditions is being explored by the first author.

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Responses of Pacific Herring, *Clupea harengus pallasi*, to Some Underwater Sounds

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We describe the behavioral responses of net-penned Pacific herring (*Clupea harengus pallasi*) to a variety of tape-recorded sounds. Sounds recorded in the field from a herring fishing fleet included moving and stationary (idling) vessels, sonar, echo sounder, and deck gear. Natural sounds included rain on the water surface, gull (*Larus* spp.) cries, killer whale (*Orcinus orca*) vocalizations, barks of Steller's sea lions (*Eumetopias jubatus*), and sounds made by herring themselves. Sounds of more uniform structure were created with an electronic synthesizer and played back to herring to determine the relative effectiveness of various combinations (triads) of amplitude and frequency (increasing, decreasing, constant) and temporal pattern (continuous, regularly, or irregularly pulsed tones). Herring did not respond visibly to any of the taped sounds of natural origin or to sonar or echo sounders. There were three categories of negative response given to other sounds. Avoidance responses were elicited by sounds of large vessels approaching at constant speed, by smaller vessels but only when on accelerated approach, and by 11 different triads of the electronically synthesized sounds. Alarm, and less frequently Startle, were both elicited by those electronic sounds with an essentially instantaneous rise time in amplitude. Herring produced Chirps and Whistles in addition to feeding and hydrodynamic noises. Chirps consisted of one or several bursts of pulses in the range 1800–3200 Hz and occurred in bouts. Whistles were narrow-band continuous (unpulsed) sounds of 1600–2000 Hz. Captive herring showed no response to playbacks of these sounds.

Nous décrivons les réponses comportementales de harengs du Pacifique (*Clupea harengus pallasi*) en parcs en filet à divers sons enregistrés sur magnétophone. Les sons enregistrés sur place à partir de bateaux de pêche du hareng comprenaient ceux émis par les bateaux en déplacement ou stationnaires (moteur au ralenti), les sonars, les échosondeurs et les engins de pêche sur le pont. Les sons d'origine naturelle comprenaient ceux de la pluie sur la surface de l'eau, le cri de goélands (*Larus* spp.), des vocalisations d'épaulards (*Orcinus orca*), des aboiements d'otaries de Steller (*Eumetopias jubatus*) et des sons produits par les harengs eux-mêmes. On a exposé les harengs à des sons plus uniformes produits par synthétiseur électronique afin de déterminer l'efficacité relative de diverses combinaisons (triades) d'amplitudes et de fréquences (croissante, décroissante et constante) et d'allures temporelles (sons pulsés ou continus réguliers ou irréguliers). Les harengs n'ont pas présenté de réactions visibles aux sons enregistrés d'origine naturelle ou à ceux des sonars et des échosondeurs. Les réponses négatives aux autres sons se divisaient en trois catégories. Des réponses d'évitement étaient provoquées par les sons émis par les gros bateaux s'approchant à vitesse constante, les petits bateaux s'approchant à grande vitesse et par 11 des triades de sons synthétisés électroniquement. Des comportements de peur et, moins fréquemment, de surprise étaient provoqués par les sons électroniques dont la caractéristique essentielle était une augmentation instantanée de l'amplitude. Les harengs émettaient des stridulations et des sifflements en plus des bruits qu'ils font lorsqu'ils s'alimentent et des bruits hydrodynamiques. Les stridulations consistaient en une ou plusieurs vagues d'impulsions de la gamme des 1800–3200 Hz et se produisaient par poussées. Les sifflements étaient des sons continus (non pulsés) à bande étroite de la gamme des 1600–2000 Hz. Les harengs en parc n'ont pas réagi à ces sons.

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The Pacific herring, *Clupea harengus pallasi*, is the basis of a large roe fishery on the west coast of Canada and the northwestern United States. Schools of herring migrate into shallow water in late winter to spawn intertidally and subtidally. Fleets of seine and gillnetting boats wait for them on traditional spawning grounds and capture them before they spawn. Recent fluctuations in herring biomass stimulated interest in the possibility that the fish were avoiding underwater noises generated by fishing vessels and gear. Accordingly, we examined the behavioral responses of Pacific herring to a variety of underwater sounds.

The importance of clupeids as food fishes has led to many studies of their biology. Most investigations of clupeid hearing have concentrated on Atlantic herring (*C. harengus harengus*). Studies on hearing in Pacific herring have not been reported to date, but morphological similarities in the auditory apparatus of this subspecies (Popper and Platt 1979) suggest the existence of similarities in hearing abilities. Examining neural activity in the

acoustic region of the medulla, Enger (1967) found Atlantic herring to be sensitive to sinusoidal pure tones over a considerably wider frequency range than most other non-ostariophysine fishes, although the low threshold (75–80 dB re 1 μPa, or dBμPa) between 30 and 1200 Hz rose sharply to 120 dBμPa as the frequency approached 3000 Hz. In behavioral studies, Olsen (1969, 1976) determined Atlantic herring to be capable of directional hearing at distances of 15–400 m (the limit of testing) from a sound source. A response was obtained to frequencies up to 10 000 Hz, but above 6000 Hz the response became nondirectional. Signals below 500 Hz elicited stronger responses than signals of higher frequencies. All stimuli had to be 20–30 dB above background before a visible response occurred. Blaxter et al. (1981b) found that even from a sound pulse of ≤2 ms, Atlantic herring could obtain sufficient information to determine the amplitude and general location of the sound. There seems to be little doubt, therefore, that Atlantic herring can hear sounds over a wide range of frequencies and can determine the location of a sound source. Other physiological work on the clupeid acoustico-lateralis system has been summarized by Blaxter et al. (1981a).

Behavioral responses of Pacific herring to sound have not been reported but those of Atlantic herring have been observed by several investigators. Atlantic herring were not attracted to any of the natural or artificial sounds presented, and responded negatively to some. Several behavioral elements, some of which occurred nearly simultaneously, were typical of the negative reaction: pack, polarize (all the fish face in the same direction), increase swimming speed, dive, and speed away from the sound source (Hering 1968; Olsen 1969). Low-frequency tones were avoided more readily than high-frequency ones (Blaxter and Holliday 1958; Hering 1968; Olsen 1970). Noise or relatively broad-band sound proved to be more effective than pure tones in some cases. Pulsed sound was more effective than a continuous tone (Hering 1968; Olsen 1970; Blaxter et al. 1981b). However, commercial echo sounders and sonar, which emit pulses of very high-frequency sound, produced no reactions whatever (Moulton and Backus 1955). Loud sounds were more effective than soft ones, but the fish sometimes adapted even to very loud low-frequency sound if intensities were constant. If the amplitude was slowly increased, a gradually increasing number of fish moved away from the source; if the amplitude increase was rapid, the number of fish avoiding the sound also increased rapidly (Olsen 1970). Habituation to a stimulus occurred if stimulus repetition rate was frequent enough, but complete extinction of the response was rare (Olsen 1976).

No studies have been made of sound production in Pacific herring nor of their responses to sounds of biological origin. Whistling sounds of 6000–7000 Hz have been recorded at night from areas where schools of Atlantic herring have been detected (Murray 1831; Freytag 1961), and Freytag (1964) suggested that these were hydrodynamic sounds made by sharply veering schools. However, hydrodynamic sounds are typically of low frequency (Tavolga 1967), making the accuracy of this interpretation doubtful. Atlantic herring did not react visibly to playback of the Whistles (Hering 1968).

The present study had three objectives. First, sounds made by fishing vessels and several items of gear, as well as various sounds of natural origin, were recorded on traditional Pacific herring spawning grounds just before the opening of the 1982 roe fishery. Selected recordings were played back to herring in net pens to determine their behavioral responses. Second, electronically synthesized sounds were presented to examine the effectiveness of different combinations of amplitude, frequency, and temporal pattern on response. Third, observations were made during feeding, schooling, and reproductive behavior in wild and captive fish to determine if sound production was associated with these activities.

Materials and Methods

All test fish came from a single stock of about 500 adult herring that had been captured by seine net in Stuart Channel, B.C., and transported 30 km in a partially submerged enclosure to the Pacific Biological Station fish farm in Departure Bay. The transfer procedure from seine to live-barge is described by Brett and Solmie (1982). Stock fish were held in a rectangular net pen (30 × 10 × 7.6 m deep) from January through April 1982. The depth under the pen was 8 m at mean low water.

Recording Procedures

Recording equipment consisted of a DC-powered cassette tape recorder (Sony TC-K81; frequency response 30–17 000 Hz ± 3 dB) and hydrophone (Celesco Industries LC-34, frequency response 25–20 000 Hz) with matching preamplifier. All field recordings were done from a small seiner, which was shut down during taping. Hydrophone depth was 25–30 m, as this was the depth at which herring schools were observed travelling during the day.

The categories of vessels and gear from which sounds were recorded are listed in Table 1. Tapes of moving vessels always included departure from as well as approach to the hydrophone. The distance of each vessel from the hydrophone was determined by radar at the start of taping and at 3-min intervals thereafter for moving vessels. A Wesmar SS-165 sonar unit was recorded while it was operating from a quiet anchored ship 0.2 km away. The upper frequency cutoff (17 kHz) of the tape recorder was well below the 165-kHz carrier frequency of the sonar. However, recordings captured the envelope of the pulsed sonar transmission and any sounds produced by raising or lowering the sonar unit in its hull mounting well. A recording was also made of a hull-mounted echo sounder (EPSCO 28 kHz). Sonar and echo sounder recordings were presented to the fish on one tape.

Several natural sounds were present in field recordings of background noise: rain on the water surface, cries of several species of gulls (*Larus* spp.) floating on the water, and barks of swimming Steller's sea lions (*Eumetopias jubatus*). These, two types of sounds recorded from captive herring, and a pre-recorded tape of sounds from a pod of killer whales (*Orcinus orca*) were also played to the fish. Measurement of the background noise level during each field recording and subsequent calculations showed signal strength to be 4–10 times greater than background. Except for killer whale sounds, the intensity levels of natural sounds are omitted because they were too close to background levels to permit measurement.

Tapes of electronic sounds were made using a Serge modular synthesizer, which eliminated switching transients. The tapes comprised 11 combinations of the variables amplitude, frequency, and temporal pattern (Table 2). Each variable was manipulated in one of three ways to create different sounds. Temporal pattern, for example, was presented as a continuous tone (P), regular pulses (PR), or irregular pulses (PI). For some sounds, amplitude (A, recorded sound pressure level of 102 dBμPa) and frequency (F, 200 Hz) were fixed. In others,

TABLE 1. Sources, frequencies, and estimated pressure levels of field-recorded sounds, and estimated projected levels to test herring.

Treatment No.	Sound source and vessel size (m)	Major frequency bands (kHz)[a]	Minimum distance from hydrophone (km)	Estimated sound pressure levels at hydrophone[b]	
				Recorded (dBμPa)	Projected (dBμPa)[c]
1	Drum seiner (18)	0–1.9	1.6	98	112
2	Gill-netter (12)	0.5, 1.0, 1.5, 2.0	0.8	92	105
3	Table seiner (20)	0–1.5	1.2	120	107
4	25-hp skiff (3)	0.5, 1.5–2.0	0.8	100	105
5	Three stationary seiners (~15)	0–2.0	2 @ 4.8 km 1 @ 1.6 km	100	109
6	Troller (15)	0–1.8	0.4	100	111
7	40-hp gillnet punt (7)	2.0, 3.0	0.09	95	105
8	Stationary seiner (20):				
	Auxiliary engine	0.5, 1–1.5, 2.0, 3.0		94	105
	Main engine	0–0.5, 1.5		95	105
	Hydraulic winch, bilge pump, and main engine	0–0.8, 1.1–1.8, 2.2–2.5		100	107
9	Sonar		0.2	—	—
	Echo sounder		0.02	—	—

[a]Analyzing filter bandwidth: 22.5 Hz.
[b]Calibration coefficients determined at 300 Hz.
[c]Projected intensity of *Orcinus orca* sounds: 115 dBμPa.

TABLE 2. Summary of mean (±SE, n = 18) response duration and response category shown by Pacific herring to electronically synthesized sounds. Underscores denote the different variable forms in each pair member. NS = not significant.

Pair	Triad No.	Triad form	Mean response duration (s)	Two-way ANOVA significance level	No. of groups in response category			
					Alarm	Avoid	Startle	No response
I	1	A:F:PI	20.0±2.4	$p < 0.025$	6	2	1	0
	2	A:F:PR	12.4±1.6		0	9	0	0
II	3	A:F:P	8.0±1.8	$p < 0.005$	1	4	1	3
	1	A:F:PI	15.9±1.4		1	8	0	0
III	4	AI:F:PI	3.3±0.8	$p < 0.001$	0	3	0	6
	5	AD:F:PI	11.4±1.9		1	7	0	1
IV	6	A:FI:PI	10.0±1.9	NS	3	4	1	1
	7	A:FD:PI	9.5±1.6		1	4	1	3
V	8	AI:FD:PI	3.6±1.2	NS	0	4	0	5
	9	AI:FI:PI	6.6±1.3		0	5	0	4
VI	10	AD:FD:PI	6.3±1.1	$p < 0.025$	0	5	2	2
	11	AD:FI:PI	12.2±1.0		4	4	1	0
Category totals					17	59	7	25

amplitude or frequency increased (AI or FI) or decreased (AD or FD) over the ranges 75–116 dBμPa and 200–1000 Hz. Preliminary experiments indicated that these amplitude and frequency ranges were readily detected by herring. Each stimulus combination (a triad) is described by appropriate notations in Table 2 (e.g. A:FI:PR indicates fixed amplitude, increasing frequency, regular pulses).

Projected sound pressure levels were as follows: A, 111 dBμPa; AI, background level (>75 dBμPa) to 111 dBμPa; AD, 111 dBμPa to background.

The duration of a triad was 15 s. For amplitude and frequency modulated triads, the change in these variables was approximately 12 dB per octave. Pulse width in triads ranged from 0.15 to 1.7 s, with rise and decay times of 32 and 70 ms, respectively. There were 17–22 pulses in triads. Interpulse intervals ranged from 0.15 to 0.5 s.

Certain triads incorporated some of the properties of vessel sounds. One example is the pair AI:F:PI and AD:F:PI. As long as the acoustic path between vessel and hydrophone is clear, sound from a vessel approaching at constant speed from a distance of a few kilometres generally increases monotonically in amplitude (AI). Frequency remains constant (F). A vessel departing at constant velocity emits sound of constant frequency (F) and decreasing amplitude (AD). The choice of PI over PR was arbitrary. A second example is the pair AD:FD:PI and AD:FI:PI. Changes in frequency occur when a vessel alters

speed, due mainly to changes in engine and propeller speed. A vessel making an accelerated departure from an object emits sound that decreases in amplitude (AD) but increases in frequency (FI); if the vessel slows down while moving away, the frequency decreases (FD). The choice of PI over PR was again arbitrary, although when speed is changed pulse repetition rate changes as well.

Herring were monitored for sound production under the following conditions: individuals, small groups, and schools (100–1000 fish) in circular fiberglass (4000 L) or rectangular glass (100–1000 L) tanks, individual fish trapped in gill nets during the roe fishery, schools in net pens in the sea in the daytime, and an unconfined school of wild herring at night.

The peak-to-peak voltage of both recorded and projected sounds was measured with a voltmeter at the tape recorder output (fixed gain of 0.4) and approximate pressure levels calculated. The peak-to-peak voltage of the same sounds as projected by the speaker was measured at the output of the preamplifier with the hydrophone at the center of the playback pen. Pressure levels for recorded and projected sounds are presented in Table 1.

Playback Experiments

The Sony unit, when used for playback, was connected to an underwater sound projector (U.S. Navy model J-9, effective frequency response of 40–20 000 Hz) via an amplifier (Advent 300). The hydrophone was placed in the center of the pen and connected to a headset to monitor the levels of projected sounds and ambient noise.

The experimental pen was cubical, 3.3 m on a side, and situated inside a shed on the fish farm. The depth under this pen was also 8 m at mean low water. The speaker was positioned just outside the pen at 1.65 m depth. All work was done during the day in natural light. Water visibility was at least 6 m throughout the study. Ambient noise levels were always under 75 dBμPa during playback experiments.

Nine experimental groups, each containing 500 herring, were tested. A group was placed in the experimental pen in the late afternoon and left overnight to acclimate. Testing began the next morning and continued throughout the day. After testing, the group was removed and a new group of 500 fish was transferred from stock pen to experimental pen.

Two playback experiments, one using the field recordings and the second the electronic sounds, were performed on each group. Four groups received field tapes in the morning and electronic tapes in the afternoon; the order was reversed for four other groups. The ninth group received only electronic tapes due to temporary equipment failure. Detailed observations of group behavior were made before and throughout playback and were correlated with the contents of the tapes. Control tests, carried out at the beginning and end of each playback, consisted of a 10-s playback of blank tape during which only machine and tape noise was projected to the fish. Lowest pressure levels of all projected sounds were adjusted to be at least 30 dB higher than the ambient noise level at the hydrophone.

Field tapes (=treatments) varied in length from 0.5 to 3 min. Order of treatment presentation was randomized for each of the nine groups, and the position of the speaker around the four sides of the pen was varied at random for each treatment. Preliminary work showed that small schools of herring returned to prestimulus behavior in 5–10 s following 10-s exposures to pure tones. The nine treatments were separated by 10-min silent intervals to ensure return to prestimulus behavior between treatments. The noises of natural origin were contained in the background portions of some of the field tapes. Their inclusion had not been planned, but we felt it desirable to take advantage of the opportunity thus afforded to see whether the herring would respond to a wider variety of sounds present in the environment. However, sound pressure levels were adjusted only for vessel and gear noise. The recording of killer whale sounds was played to four groups before and to four groups after presentation of the field tapes.

Separate tapes were made of each of the 11 triads of electronic sounds (Table 2). Each tape contained five 15-s repetitions of a triad; consecutive repetitions were separated by 30-s silent periods. One form of PI was used for all five repetitions of a triad. The triads were presented as six pairs; A:F:PI was tested twice, once against A:F:P and once against A:F:PR. The two triads constituting a pair differed only in one variable, e.g. AD:FI:PI–AI:FI:PI. Pairs were presented in random order to each group, and the position of the speaker was varied randomly for each pair. Each pair was separated from the next by a 10-min silent interval and, within a pair, tapes were alternated for each group and separated by 2 min of silence.

Data Analysis

Recorded sounds were analyzed using a Kay Elemetrics 7029A spectrum analyzer and an oscilloscope. Only sounds recorded in net pens or in the field were subjected to spectrographic analysis.

Reactions to sounds were of three types: Avoid, Alarm, and Startle (see Results for description). The duration (in seconds) of the responses Avoid and Alarm was the measure used to quantify the effect of a sound on the fish. Each group of herring served as its own control. The observer sat quietly by the pen and wore earphones to monitor the sounds as they were projected to the fish.

Responses to the field tape treatments were evaluated using nonparametric statistics (Siegel 1956) and two measures of effectiveness: (1) the number of groups responding to a given treatment and (2) the percent of responding groups habituating to that treatment.

For the electronic sounds we used two-way ANOVAs to determine whether one pair member was more effective than another, with duration of the first and fifth responses as the test measure. Habituation was also investigated. The criterion used for habituation to a triad was a response of shorter duration to the fifth repetition of that triad than to the first one. Double testing of A:F:PI also permitted comparison of the responses of the nine groups to the two exposures to this triad.

Results

Behavioral Responses to Sounds

A group of herring typically formed a single school and spent most of the time circling the perimeter of the experimental pen, alternately clockwise and counterclockwise. The fish never avoided the area around the speaker when it was silent, and it was not known whether they saw it. Sporadic feeding occurred while schooling. The school only broke up to feed if plankton was abundant.

Herring were not attracted by any of the acoustic stimuli we used. Although they made no response whatever to some sounds, they did respond negatively to many. Mildly negative behavior, termed Avoidance, was defined as one response type.

If the fish had been feeding heavily, they stopped and sank about 1 m below the surface, interindividual distances lessened and became more uniform, and polarization increased resulting in a fairly compact school. The school then moved slowly away from the sound source, swimming directly to the far side of the pen. Fish that were schooling but not feeding before Avoiding a sound maintained formation while moving away from the sound source.

The second type of response was termed Alarm. Alarm contained elements of Avoid but these appeared at extremely high rapidity and intensity. An Alarmed group packed, polarized, and fled away and downward from the stimulus source regardless of its previous behavior. It might dive to the bottom of the pen and lie motionless, dive to midwater and then repeatedly and quickly change direction, or dive to midwater and break into a number of smaller schools, each of which fled in a different direction and changed direction repeatedly.

Schools that did not habituate to a given stimulus kept circling at a maximum distance from the speaker. They returned immediately or nearly immediately to the area adjacent to the speaker when the sound ended.

A third type of response was Startle, defined as a single powerful flexion of the body followed by a 5- to 10-s period of faster swimming. A fish did not change its original heading when it Startled. Occasionally, one or more fish in a group Startled, usually either when a loud tape was first turned on or in response to stimuli of unknown origin in the water around the pen. Startle was not followed by Avoidance or Alarm. School formation was not affected by the Startle response.

Sounds Made by Pacific Herring

Pacific herring produced two kinds of sounds, termed "Chirps" and "Whistles." Chirps resembled high-pitched gurgles and were heard frequently from schools of 250–5000 fish in net pens. A Chirp (Fig. 1A) consisted of one but more often several bursts of pulses. The widest frequency range of a burst extended from 1800 to 3200 Hz; however, most Chirps were in the range 2600–3800 Hz. Temporal composition was variable. One common pattern was a long burst followed by several shorter ones, and another (shown in the example) was several bursts of approximately equal length. Chirp signal strength could not be measured accurately because the sounds were very close to background level even when the hydrophone was placed within a school, but they were easily heard through the headphones. In a sample of 26 Chirps taken from 11 different schools, average Chirp duration was 3.4 s but the range was wide (0.5–10 s).

Individuals and groups of fish were monitored for 2 h each to determine Chirp rate. This was found to vary with the number of fish in the group. Chirps were not made by isolated fish ($n = 13$) and were heard only once from 1 of the 12 small groups formed by sequential addition of the fish that had been monitored singly. From two groups each containing 250 fish, 52 and 156 Chirps were heard, and a total of 492 Chirps from two groups of 5000 fish each. The latter figure is conservative: due to the large size of the pens containing these larger groups and the low amplitude of the Chirps, it is unlikely that all the Chirps made by these fish were heard.

Chirps were heard almost exclusively from calmly schooling fish. They were not heard when a school broke up to feed nor during Alarm, Avoid, or Startle responses. Chirps occurred in bouts of varying duration but neither bouts nor interbout silent intervals could be correlated with changes in school density, speed, direction, or depth, in cloud cover or precipitation, or with a 2-h period following heavy feeding on plankton or laboratory chow. The single Chirp heard from a group of four fish swimming in loose aggregation was accompanied by a brief pause by all individuals but by no other change in behavior. Chirps were not produced when a fish coughed, yawned, or snapped at an object in the water.

Whistles (Fig. 1B) were recorded in Mayne Bay, Barkley Sound, B.C., on 6 March between 00:30 and 01:30, from a motionless school of fish located by echo sounder and identified as herring by the vessel's crew. Whistles, like Chirps, were so close to background in intensity that their amplitude could not be measured. In a sample of 22 Whistles, mean duration was 0.9 s (range 0.5–1.8 s) and the frequency range was 1600–2000 Hz; thus, the range of frequency and duration was much narrower than for Chirps. The temporal pattern of Whistles was also far more uniform than that of Chirps, taking the form of a nearly continuous, narrow-band tone that slowly rose in frequency at the end. Like Chirps, Whistles were heard in bouts. They did not fit the description of whistles reported by Murray (1831) or Freytag (1961).

Herring in net pens were not monitored at night. On four occasions during daytime observations, however, Chirps graded into Whistles, which sonagraphic analysis showed to resemble the Whistles recorded in the field. During night taping in the field, three Chirps were also heard. These observations further support the idea that herring were the source of the Whistles.

Live herring caught in a gill net during the fishery were monitored for sounds. Many of the fish were held by the mesh at the anterior body and appeared to be ventilating normally. No sounds were heard from them over a period of 0.5 h.

Herring produced two kinds of incidental noise. Percussive sounds (Fig. 2A) were heard when the fish fed on commercial laboratory chow but not when they ate live or frozen plankton, suggesting that the sounds were due to food hardness. When fish feeding on laboratory chow were close to the hydrophone, jaw movements were easily correlated with the feeding sounds. Hydrodynamic sounds (Fig. 2B) were heard when large schools in net pens suddenly accelerated or abruptly changed direction. These sounds were low-pitched roars with major frequencies below 500 Hz.

Responses to Playback of Sounds of Vessels and Gear

Sonagraphs of vessel sounds indicated that the larger the ship, the lower the frequencies in which the acoustic energy was concentrated (Table 1). Sound pressure levels also increased with vessel size. The larger vessels were audible at greater distances: the smaller the craft, the closer it had to come to the hydrophone before the amplitude of its sound approached that of the largest ships (Table 1). The echo sounder produced regular broad-band clicks (50–2000 Hz) whose source was the stepping motor inside the sound dome (W. N. Tavolga, Mote Marine Laboratory, Sarasota, FL 32577, pers. comm.). Sonagraphic analysis of the sonar unit was not possible, since the unit was inaudible at 0.2 km and the sounds of raising and lowering it approximated background intensity levels.

Avoidance was the main response to playback of the field recordings, and was always directional, i.e. away from the sound source. Startle was seen occasionally and Alarm was never observed. Significant differences existed in the number of

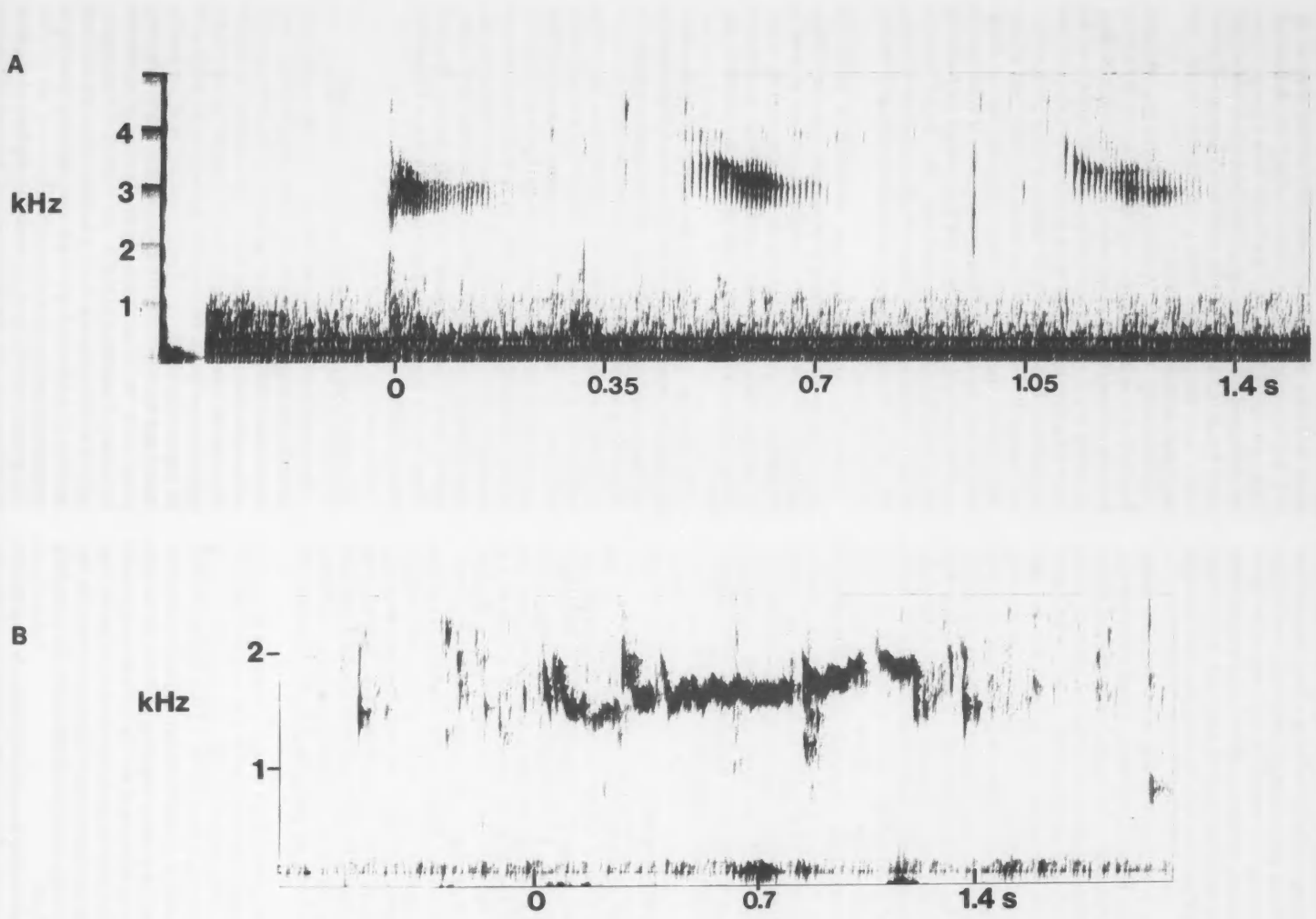

FIG. 1. Sonagraphs of (A) Chirps and (B) Whistles produced by Pacific herring. Analyzing filter bandwidth is 300 Hz for Chirps and 150 Hz for Whistles.

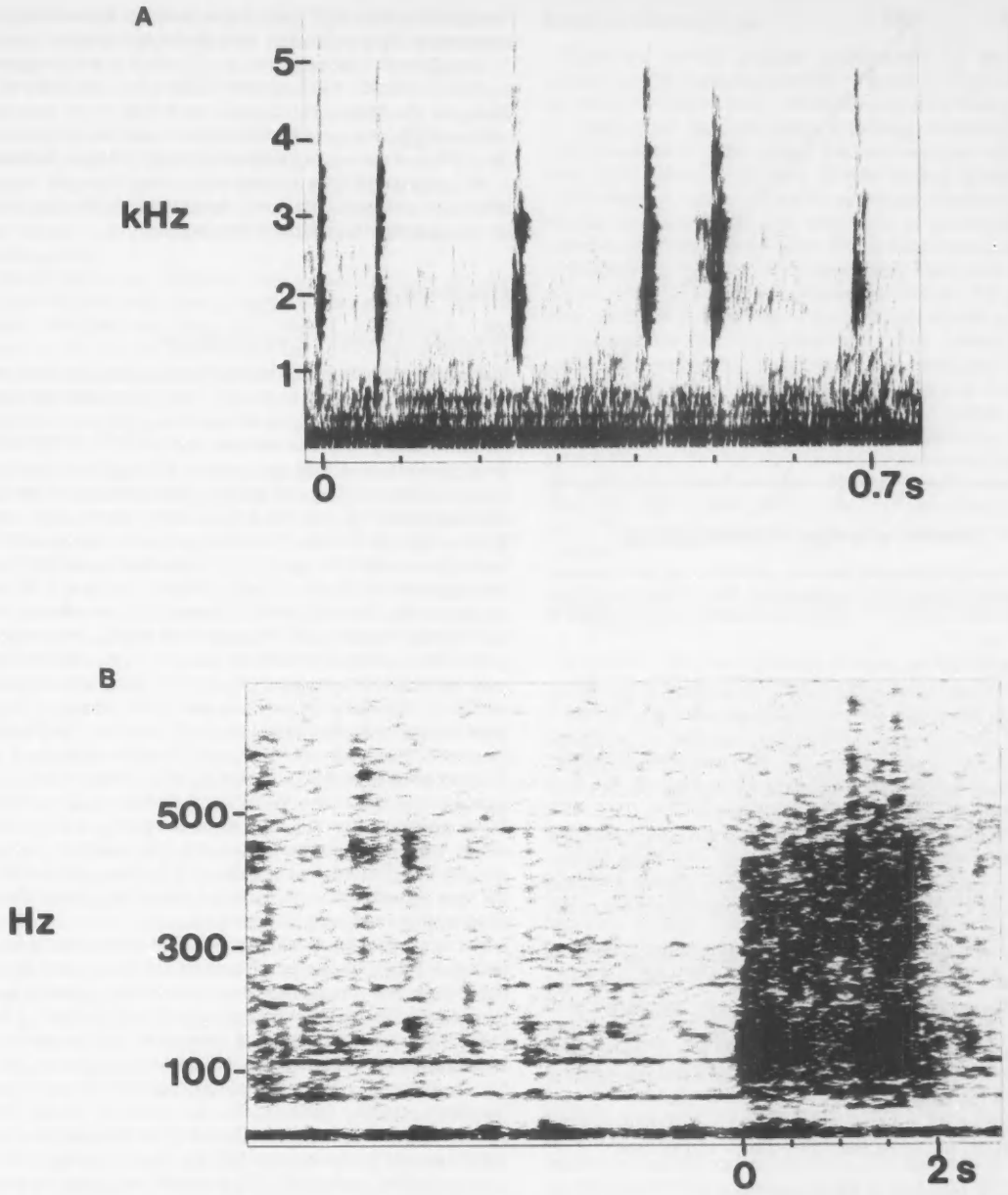

FIG. 2. Sonagraphs of (A) feeding sounds and (B) hydrodynamic sounds produced by a veering school of Pacific herring. Analyzing filter bandwidth is 300 Hz for feeding noises and 5.6 Hz for hydrodynamic sounds.

groups responding to each of the nine treatments (Friedman two-way ANOVA, $P < 0.05$). A strong inverse correlation (Fig. 3) also was found between the number of groups that Avoided a treatment and the percent of those groups that habituated to that treatment (Cochran Q test (Siegel 1956), $P < 0.005$); i.e. the more effective a sound was in producing a response, the lower the probability that the fish would habituate to that sound. Sounds made by large vessels approaching at constant speed (treatments 1, 3, and 6, Table 1) were Avoided by most groups, and only about 25% of these groups habituated to these noises (Fig. 3). Avoidance ended within 10 s after the vessel began departing and its noise began diminishing in intensity, but although the fish returned to the vicinity of the sound source they did not approach the surface again for 1–3 min more.

Fewer groups responded to the sounds made by smaller vessels. Sounds of the 25-hp skiff (treatment 4, Fig. 3) were Avoided only by two groups and then only during accelerated

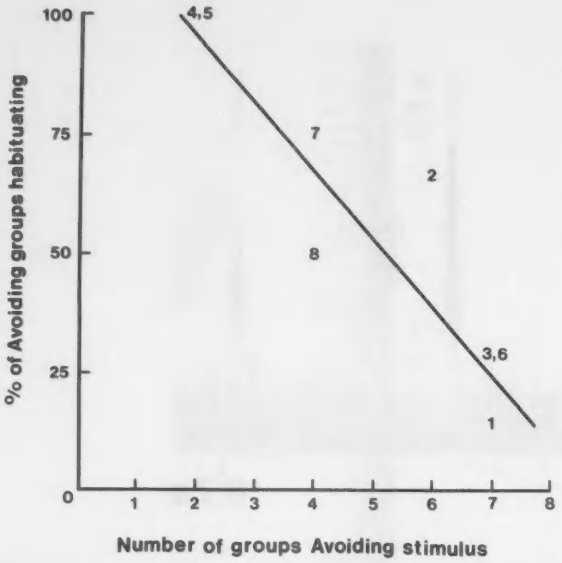

FIG. 3. Inverse relationship between Avoidance and habituation of Pacific herring to sounds of vessels and gear. The numbers in the figure denote the sound sources (=treatments) presented and are defined in Table 1.

approach. Three of the four groups responding to the 40-hp gillnet punt habituated to its sound (treatment 7, Fig. 3).

The 2-min recording of stationary seiners with engines running was Avoided by two groups for 15 s each (treatment 5, Fig. 3). Some individuals in two other groups Startled but then immediately returned to prestimulus behavior.

The recording of the sonar unit operating and being raised and lowered had no visible effect on the fish. Schooling herring showed no reaction to sonar beamed directly onto them from a silent vessel 15 m away. None of the groups responded to the echo sounder recording.

Four of the eight groups responded to sequential playback of engines and gear (treatment 8, Fig. 3). Two of these groups Avoided the speaker when the auxiliary engine was started, then returned, Avoided the speaker again at the start of the main engine, and then returned and ignored the rest of the sounds. The other two groups schooled some distance from the speaker throughout the tape.

The herring did not visibly respond to any of the sounds of natural origin, including their own Chirps and Whistles.

Responses to Playback of Electronic Tapes

Significant differences in the mean duration of the negative response were found between pair members in four of the six pairs of triads (Table 2). PI represented a more aversive stimulus than either PR or P (pairs I and II, respectively). AD was more effective than AI (pair III). No differences were seen in response to FI and FD when amplitude was held constant (A) or increased (AI). However, when amplitude was decreased (AD), FI was more effective than FD (pair VI). When the triad AD:FD:PI was presented, the number of fish Avoiding the speaker slowly increased with decreasing frequency of the sound; in contrast, the response to AD:FI:PI was immediate and vigorous.

Approximately half the responses were in the category Avoid. Examination of Table 2 also indicates that within pairs, responses of longer duration were higher in intensity (Alarm).

Comparison of the responses of all groups to both exposures to A:F:PI revealed no significant difference in mean duration. However, the behavioral response to A:F:PI when associated with A:F:PR was considerably more vigorous (6 Alarm, 2 Avoid) than it was when paired with A:F:P (1 Alarm, 8 Avoid).

Although habituation to some triads seemed to occur (i.e. the fifth response to some triads was shorter than the first response), overall statistical significance was lacking.

Discussion

Properties of Sounds Eliciting Responses

Our study shows Pacific herring to be capable of directional and selective responses to sounds. The magnitude, direction, and rate of change of amplitude were among the most important factors affecting response duration and intensity. Loud sounds were more effective than soft sounds. As amplitude is affected by vessel size, under similar acoustic conditions and at the same distance and speed, the sound of a large vessel will be louder than that of a small one. Small vessels had to be closer to the hydrophone before the intensity of their sounds matched that of the larger vessels (Table 1), suggesting that the larger the ship, the greater the distance at which it could influence the behavior of a school. Sounds made by large approaching craft were far more effective than sounds of constant or decreasing amplitude made by stationary or departing vessels. Although electronic sounds incorporating A or AD elicited longer and more intense negative responses than those containing AI, each repetition of a triad was preceded by silence, so that triads containing A and AD were actually heard by the fish as sudden loud sounds whose intensity was then either maintained or decreased. Sounds of departing vessels, on the other hand, were always preceded by sounds of the same craft approaching so that amplitude increase was gradual. The fish thus responded to increases in amplitude, and their response increased in intensity and duration as the rate of change of amplitude increased.

Herring responded to both the pure sine waves and the broad-band field sounds, but spectral content did affect response. The larger the vessel, the more of its acoustic energy is in the lower frequencies (Table 1). Where sounds of a small and a large vessel were presented at equal intensities, the sounds of the latter were most effective (e.g. gill-netter vs. seiner) (Table 1; Fig. 3), suggesting that the reaction of the fish was to the lower frequency sounds. Furthermore, the responses to electronic sounds suggest that the hearing threshold for frequencies around 200 Hz may be below that for 1000 Hz. The combination AD:FI was more effective than AD:FD, probably because in the former case the loudest portion of the sound coincided with the lowest portion of the frequency envelope, whereas in the latter case the lowest frequency was presented at very low amplitude. The lack of difference in responses to FD and FI when presented with AI may be related to the gradual rise in amplitude and the short stimulus duration, but the reason for the lack of difference in responses to FD and FI when presented with A is not clear.

Irregular pulses (PI) were more effective than either regular pulses or continuous tones (PR, P). Abrupt changes in temporal rhythm accompany sudden change in a vessel's speed and also occur when engines, propellers, or motor-driven deck gear are started, speeded up, or shut down. Although the importance of these changes compared with the importance of changes in

amplitude cannot be determined from this study, substantial evidence exists to support the idea that temporal pattern is more important to a fish than the frequency spectrum of a sound (e.g. Winn 1964; Hawkins and Myrberg 1983). The sounds that fishes use in intraspecific communication differ in temporal pattern far more than they do in frequency characteristics. Parenthetically, the response to PI when paired with PR was stronger than it was when paired with P, although not significantly longer in duration (Table 2), suggesting that some order effects may have persisted in spite of our attempts to minimize them.

The absence of any visible response to the recordings of sonar and echo sounder or to directly applied sonar indicates that use of these instruments in the field should not affect herring behavior. The lack of response on the part of other fishes to sonar and echo sounders is well-documented (Moulton and Backus 1955).

Habituation to Sounds

Postspawning Atlantic herring appear to be more sensitive to a variety of stimuli than fish that are spawning or about to spawn (Mohr 1964; FAO 1970), and Pacific herring may share this trait. However, even though 80% or more of the fish in each group had spawned prior to the start of this study, they habituated to many of the field-recorded sounds. Furthermore, they were never seen to react visibly to sounds made by a variety of boats moving about in the vicinity of the Station about 0.2 km from the fish farm, or to the sounds of small boats traveling between the farm and the Station, even when those boats were operating within 15 m of the test pen. This probably indicates habituation to the acoustic environment, since the fish had been held on the farm for about 2 mo prior to the study and the sounds of the boats were not associated with attempts to capture or disturb the fish. Fishermen refer to the need for herring newly arrived on the grounds to "harden," which they define as the process by which schools become more accustomed to the presence of moving vessels, and will put off fishing for several days so that hardening may take place. Hardening may be synonymous with habituation. This delay in fishing is more common along the open coast than along the inner coast between Vancouver Island and the mainland, suggesting that exposure of the herring to the noise of continuous vessel traffic while the fish migrate through these inner waters might assist the hardening process. However, the groups did not demonstrate statistically significant habituation to presentations of electronic sounds, possibly because presentation time was too short.

The effect of many vessels operating simultaneously on herring schools entering the spawning grounds is not known, nor is it known whether fleet concentration in a few areas over several seasons can influence the fish away from those areas for a prolonged period of time. However, the fish Avoided the sounds of large approaching vessels on first exposure, and habituated least to them. The seiners are the largest vessels in the fleet. They actively pursue herring schools and operate directly over them. The gill-netters do not fish actively and moreover are usually removed from the fishing area, serving instead as packer boats for the gillnetted herring. The gillnet punts travel between the gill nets and the packer boats. Recorded sounds of the punts and of smaller skiffs produced the fewest and shortest responses. Trollers do not participate in the fishery, although some may be present on the grounds. Thus, the seiners appear to represent the major source of aversive acoustic stimuli in the fleet for the herring.

Sounds of Natural Origin

There are several possible explanations for the lack of response to any of the taped sounds of natural origin. Except for the sounds of killer whales, the others may have been projected at subthreshold intensities for the herring. Alternatively, the sounds may have been audible but may not have represented meaningful events for the fish. If wild herring indeed react to killer whale sounds, olfactory or visual reinforcement or changes in water movement may have to accompany those sounds for the response to occur. Visual reinforcement of alarm calls appears to be necessary to keep birds away from roosts or airports (Pearson et al. 1967; Murton and Wright 1968). On the other hand, the loud sounds from the large vessels needed no reinforcing stimuli to exert their effect. The context in which sounds are presented is important. If a particular sound is produced primarily at night, then playback of it in the daytime may elicit little or no response. Finally, sounds used in communication often contain nuances of frequency or temporal pattern that may be necessary to produce a response but that do not reproduce well on tape. Hering (1968) obtained no responses from Atlantic herring when he played back whistles of 6–7 kHz that had been recorded in the vicinity of herring schools.

Herring Sound Production: Possible Mechanisms and Roles in Behavior

A function for Chirps was not obvious, as schooling fish did not alter their behavior during Chirping or in response to Chirp playbacks. Partridge and Pitcher (1980) determined for several species that daytime schools are maintained primarily by vision with additional input from the lateral line system. However, since Chirps were heard only from schooling fish, they may serve as an additional mechanism for school maintenance, as has been conjectured for the swimming sounds of *Anchoviella* schools (Moulton 1960). This would not require Chirps to be produced either deliberately or continuously (rather than in bouts). Moreover, herring, like other clupeids examined, have excellent hearing, which probably assists them in evading predators. Continuous Chirps could reduce the ability to take evasive action, and this may explain why Chirps occurred in bouts.

The herring swimbladder connects posteriorly with the cloacal region through an anal duct and anteriorly with the fundus of the stomach through a larger pneumatic duct (Allen et al. 1976). As no specific body movements or any release of bubbles were seen accompanying Chirps, these sounds could arise from the passage of gases through the pneumatic duct between swimbladder and stomach. The sphincter controlling gas movement closes during feeding so that food particles will not enter the swimbladder, which could explain why no Chirps were heard from feeding herring. Sphincter closure during fright would also account for the lack of Chirps at these times, during which schooling would presumably be coordinated by the other mechanisms mentioned above. It is unlikely that Chirps reflect buoyancy adjustments, since they were not accompanied by changes in depth.

The mechanism by which Whistles are produced is not known. A function for Whistles is suggested here by the behavior of herring schools. In the daytime herring travel in compact schools at depth, but at night the schools rise in the water and spread out into flatter, more two-dimensional configurations (Blaxter and Holliday 1963) which generally

travel shorter distances and at slower speeds than during the day. Near dawn the schools again assume a compact shape and sink into deeper water. It is tempting to speculate that Whistles could help fish that are near neighbors to remain in some proximity to one another while the school is spread out, facilitating regrouping near dawn. Moreover, the structure of Whistles, unlike that of Chirps, could make it difficult for predators to localize such a school by auditory means. A sound source should be intermittent and contain multiple frequencies for localization (Marler 1959), and several studies have demonstrated that fish predators are attracted to pulsed, broad-band sounds (e.g. Myrberg 1972). Chirps are pulsed and broad-band, but Whistles exhibit several of the properties that make avian alarm calls difficult to localize: they are tuned to a narrow and (for fish) fairly high-frequency band, show very small pitch variation, and each is a continuous tone rather than pulsed. Such a role for a fish sound has not been suggested for any other species investigated and should be explored further, including recording and playback of Whistles at night using a net-penned school.

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Meteorological and Hydrographic Regulation of Year-Class Strength in Capelin (*Mallotus villosus*)[1]

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Year-class strength (YCS) in eastern Newfoundland stocks of capelin (*Mallotus villosus*), a beach spawning osmerid, during the interval 1966–78 was strongly influenced by onshore wind frequency during the period immediately following hatching (WIND) and water temperatures experienced during the subsequent period of larval drift (TEMPSUM). The exact form of the relationship was ln YCS = 16.10 − 0.19WIND + 0.19TEMPSUM, $R^2 = 0.58$. Wind conditions subsequent to hatching are known to influence both the timing of larval emergence from the beach spawning beds and the physical condition of larvae at emergence. Our analysis suggests that the influence of wind on early larval survival is also strong. The role of water temperatures during drift may be indirect, operating via its influence on food production. This could operate by altering mortality rates due to starvation or by altering growth rates which would influence swimming performance, predator avoidance, and time to metamorphosis. The strong influence of these abiotic variables, independent of parent stock size, adds further support to the hypothesis that abiotic factors operating at critical periods in larval development may be more important than spawning stock biomass as regulators of year-class size. Our findings also suggest that these critical periods must be identified and quantified at time scales relevant to individual larvae if reliable forecasting of year-class strength is to be achieved. On the other hand, the large spatial scale of the effects suggests that the space scale of individual larvae is of lesser importance in such analyses.

L'importance des classes d'âge (YCS) des stocks de capelan (*Mallotus villosus*) de l'est de Terre-Neuve, un osméridé frayant sur les plages, a beaucoup dépendu, de 1970 à 1978, de la fréquence des vents du large lors de la période suivant immédiatement l'éclosion (WIND) ainsi que de la température de l'eau pendant la dérive ultérieure des larves (TEMPSUM). La forme exacte de cette relation était ln YCS = 16,10 − 0,19WIND + 0,19TEMPSUM, $R^2 = 0,58$. On sait que les vents ultérieurs à l'éclosion influent sur l'état des larves et le moment de leur émergence des lits de frai des plages. Notre analyse indique que les vents ont aussi une forte influence sur la survie des jeunes larves. Le rôle de la température de l'eau lors de la dérive pourrait être indirect, celle-ci agissant sur la production de nourriture. Cette action pourrait prendre la forme d'une augmentation des taux de mortalité par inanition ou d'une modification du taux de croissance qui influerait sur la capacité de nage et d'évitement des prédateurs ainsi que sur la période de pré-métamorphose. La forte influence de ces variables abiotiques, indépendantes de la taille du stock parental, vient renforcer l'hypothèse voulant que des facteurs abiotiques agissant à des moments critiques du développement larvaire peuvent être plus importants que la biomasse du stock de frai comme régulateur de la classe annuelle. Nos résultats portent aussi à croire qu'une prévision fiable de la classe annuelle ne pourra être obtenu qu'en déterminant et quantifiant ces periodes critiques aux échelles temporelles des larves elles-mêmes. L'importante échelle spatiale de ces effets donne cependant à croire que l'échelle spatiale des larves elles-mêmes est moins importante lors de telles analyses.

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Forecasting recruitment to mature or exploitable stocks has long been a central problem in fishery research. Stock-recruitment models have dominated this field since Ricker's (1954) classic treatment of the subject. These models are based exclusively on biological interactions, integrate the entire life history into a single prerecruit class, and ignore potentially important abiotic influences on recruitment processes (Bakun et al. 1982). This may, in part, explain their relatively poor predictive power, although Walters and Ludwig (1981) have recently demonstrated that the approach also has statistical problems, the principal difficulty being unknown error in the independent variable (parent stock size).

[1]Contribution to the program of GIROQ (Groupe interuniversitaire de recherches océanographique du Québec).

FIG. 1. Locations of NAFO areas 2J, 3K, and 3L and of sampling sites for water temperatures. Approximate northern limit of the Grand Banks is determined by the 100-fathom contour north of Bryant's Cove.

Investigators have made several attempts to account for variance in recruitment by examining the effect of abiotic factors. For example, Nelson et al. (1977) demonstrated that onshore Ekmann transport of larvae explained a significant portion of the residual variance about the stock recruitment model for Atlantic menhaden (*Brevoortia tyrannus*); Bailey (1981), using a multiple regression approach, found that spawning stock biomass and the intensity of offshore Ekmann transport during larval drift were the major regulators of year-class strength in Pacific hake (*Merluccius productus*); Leggett (1977) showed that water temperature during the immediate post spawning period was an important cause of residual variance in the stock-recruitment model for American shad (*Alosa sapidissima*) in the Connecticut River; and Chadwick et al. (1977) demonstrated the importance of river discharge as a regulator of year-class variations in striped bass (*Morone saxatilis*) in the Sacramento River, California. While this approach leaves unresolved the problem of unknown error in the independent variable, these studies, and others, did highlight the potential importance of abiotic regulators of year-class strength in fishes.

Concurrently, the importance of abiotic factors as regulators of a variety of other biotic processes in both freshwater and marine systems has become apparent. In coastal systems in particular, short-term (days to weeks) and long-term (months to years) variation in the distribution, abundance, and production dynamics of a variety of organisms from plankton to whales have been related to the impact of large-scale meteorological influences on the ocean environment (seals, whales, and sea birds, Sergeant 1982; phytoplankton community structure, Lasker 1978; Coté and Platt 1983; zooplankton community structure, Frank and Leggett 1982b; phytoplankton biomass and production, Walsh et al. 1977, 1978; and fish production and biomass, Sutcliffe 1972; Haymand and Tyler 1980; Clark et al. 1975).

The capelin (*Mallotus villosus*), a key forage species in the Northwest Atlantic ecosystem (Bailey et al. 1977), exhibits large year to year variations in year-class strength. Year-class strength in the Northwest Atlantic Fishery Organization (NAFO) 2J3K stock (Fig. 1, 3) has been estimated to vary over 37-fold during the interval 1972–80 (Carscadden and Miller 1981). These large variations in capelin abundance, coupled with its importance as a prey species, have led to considerable interest and expectation that changes in capelin abundance would impact on the abundance and distribution of predators and potential competitors (Carscadden 1983a), as has been reported for other marine ecosystems (Daan 1978). While quantitative information is limited, some possible interactions have been identified in the case of squid (*Illex illecebrosus*) and arctic cod (*Boreogadus saida*, Vesin et al. 1981); Atlantic cod

(*Gadus morhua*, Akenhead et al. 1982); and Atlantic salmon (*Salmo salar*, Reddin and Carscadden 1981; Carscadden and Reddin 1982).

It has now been demonstrated for several fish populations that year-class strength is largely determined by the end of the larval period and that all age groups subsequently remain roughly proportional to the annual abundance of the fingerling cohort (see Cushing 1975; Dragesund and Nakken 1973; Chadwick et al. 1977; Leggett 1977). Meteorological factors, principally air temperature, solar radiation, and wind direction, together with water temperature, are major regulators of egg development rate and mortality in capelin (Frank and Leggett 1981a, 1981b). In turn, beach residence time in capelin is determined by the length of the interval between onshore winds, which trigger larval emergence (Frank and Leggett 1981a, 1982a). Larval condition at the onset of drift, and hence survival, is a negative function of beach residence time (Frank and Leggett 1981a). Food availability during drift is also widely held to be an important regulator of survival in pelagic fish larvae (Lasker 1975, 1981). Water temperatures are directly correlated with rates of biological production and thus with food availability (Eppley 1972; Tranter 1976).

These facts led us to speculate that the large-scale variations in year-class strength in capelin, which occur synchronously in populations in the eastern Newfoundland region, are due to the effect of large-scale meteorological and hydrographic variability acting directly and indirectly on the survival of larval capelin. This idea was strengthened by observed differences in the apparent survival of the 1978 and 1979 larval cohorts at our Bryant's Cove, Conception Bay, Newfoundland, study site and its correlation with year-class strength. Capelin egg densities were similar in 1978 and 1979 but larval emergence into the nearshore area was 60% higher in 1979. The frequency of onshore winds was 50% higher in 1979 resulting in shorter larval residence times. The 1979 year-class appears to be much stronger than the 1978 year-class and dominated the mature portion of the population in 1982 (Carscadden 1983b).

In this paper we report the results of a study conducted to evaluate the hypothesis that year to year variation in year-class strength of capelin is influenced by meteorological and hydrographic conditions. We examined the effects of (1) the frequency of occurrence of onshore winds during the period immediately following hatching and (2) the water temperatures experienced subsequent to the onset of larval drift on year-class strength in capelin. The analysis relates to the capelin stocks occupying the NAFO Divisions 2J and 3K (Fig. 1).

Methods

Our analysis is based on linear regression models incorporating the interval between onshore wind events during the period of beach residence by larval capelin, and water temperatures during larval drift, as independent variables and the natural logarithm of abundance of 2-yr-old capelin as the dependent variable. Nonlinear models were evaluated but proved to be inferior.

Model Development

Wind

A central assumption of the wind regulation hypothesis is that cyclonic atmospheric pressure systems generating onshore winds (and the related coastal water mass exchange that triggers

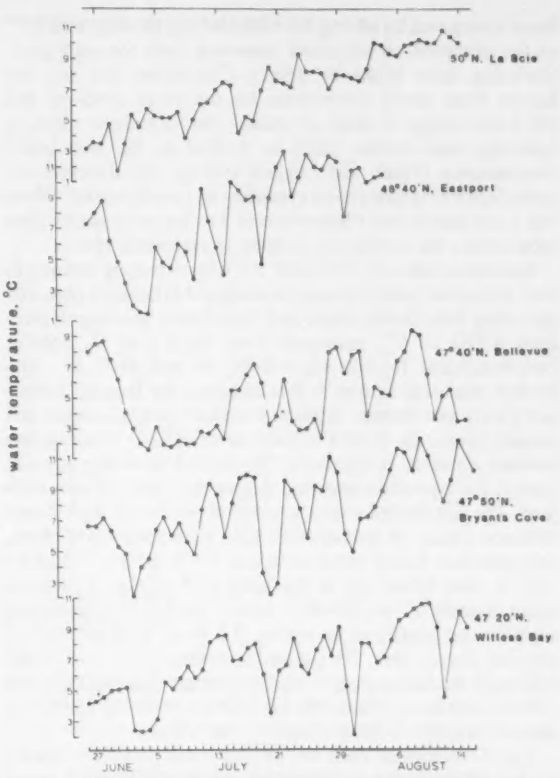

FIG. 2. Nearshore water temperatures at five capelin beach spawning sites in eastern Newfoundland, 26 June–14 August 1982.

larval emergence, Frank and Leggett 1982b, 1983) are large enough to synchronously influence water mass exchange over a large area of Newfoundland's east coast. Simultaneous recording of nearshore water temperatures at five beach spawning sites ranging over 4°40′ of latitude and ~700 km of coastline (Fig. 1) during 26 June–14 August 1982 shows this to be true (Fig. 2). Major changes in nearshore water temperatures, indicative of wind-driven water mass exchange, were virtually synchronous at all sites. The transition from rising to falling water temperatures (offshore winds) or falling to rising water temperatures (onshore winds) seldom varied by more than 1 d (Fig. 2). Larval emergence data for one of these sites, Eastport, Bonavista Bay, show a significant positive relationship between larval emergence and onshore winds ($r^2 = 0.53$) (Fig. 2). The timing of emergence was also synchronous with the daily larval emergence pattern at Bryant's Cove, Conception Bay ($r^2 = 0.62$). We have previously shown that onshore winds generate similar emergence patterns at widely separated sites and over long time periods (Frank and Leggett 1981a).

Daily wind data used in the analysis were obtained from monthly wind summaries for the St. John's, Newfoundland, meteorological station published by Environment Canada. Spawning dates and egg development rates vary between years (Frank and Leggett 1981b). This causes annual differences in the time of median hatching and hence in the timing of the critical period for larval emergence. We determined the *annual* timing of median hatching, and hence the critical period for

larval emergence by adding the estimated egg development time to the observed or estimated spawning data for each year. Spawning dates in the St. John's–Conception Bay area are known from direct observation for the years 1966–69 and 1972–82 (range 7 June–25 June). No latitudinal trend in spawning time within years is evident in the area under consideration (Frank and Leggett 1981b). We therefore assumed spawning dates to be synchronous over the coast. While this is not strictly true (differences of 1 or 2 d occur even within local areas), the assumption creates no systematic bias.

Spawning dates in 1970 and 1971, which were unknown, were estimated from an empirical relationship between observed spawning date (Julian days) and cumulative growing degree-days (GDD > 5°C measured from April 1 at St. John's, Newfoundland) for the years 1966–69 and 1972–81. The method used was similar to that employed by Burgner (1980) and Colby and Nepszy (1981) to predict spawning times and maturity rates in Pacific salmon and walleye (*Stizostedion vitreum vitreum*), respectively. We plotted spawning date (Y) against the equivalent growing degree-day value (X) for each year. The plot yielded a vertical cloud of points with high Y-axis variance (mean 16.5 June, 95% C.I. 12.5 June– 20.6 June) and restricted X-axis variance (mean 139.5, 95% C.I. 124.3–154.7). One Julian day in the latter half of June equates to approximately 10 degree-days. Spawning date in capelin can therefore be predicted to within 3 d from a knowledge of growing degree days. We equated spawning dates in 1970 and 1971 with the Julian dates most closely approximating the mean (139.5) degree-day value for the interval 1966–82 (1970: 17 June = 144.2°C-d; 1971: 2 June = 140.1°C-d).

Egg development rates are strongly and positively related ($r^2 = 0.89$) to average incubation temperatures in the beach gravel (Frank and Leggett 1981b). Daily incubation temperatures can be predicted from the equation (Frank and Leggett 1981b)

$$Y = 0.607x_1 + 0.348x_2 + 0.392x_3 + 0.142x_4 - 0.297, \quad R^2 = 0.76$$

where Y = incubation temperature (degrees Celcius), x_1 = water temperature (degrees Celcius), x_2 = hours of bright sunlight per day, x_3 = minimum daily air temperature (degrees Celcius), and x_4 = maximum daily air temperature (degrees Celcius).

This equation predicts incubation temperatures near the high tide zone on the beach where temperatures are highest (Frank and Leggett 1981b). We chose to use the high tide estimator because (1) egg densities are greatest at the high tide zone and (2) the analysis is conservative: larvae hatching slightly later from the mid and low tide zones are automatically included in the wind analysis. Daily incubation temperatures were estimated using meteorological data from the St. John's, Newfoundland, meteorological station of Environment Canada. Data from this station for 1978 and 1979 were originally used to develop the predictive equation given above. The observed or estimated spawning date was used as the starting point for this calculation and the average incubation temperature was taken as the mean of estimated daily temperatures over the following 14 d. Average incubation temperatures varied between 8 and 15°C during the period 1966–78.

Mean time to hatching (range 12–18 d during 1966–78) was derived from the equation (Frank and Leggett 1981b)

$$\ln y = 4.29 - 0.63 \ln (x + 1), \quad r^2 = 0.89$$

where y = hatching time (days) and x = average incubation temperature (degrees Celcius).

The maximum time interval between onshore winds (defined as all winds oriented north through east) during the 10-d period immediately following the estimated annual median hatching date was used as the wind input to the model. This value ranged from 2 to 10 d (mean 4.4 d). The north through east wind orientation was established a priori based on the orientation of the coastline in the 2J3K areas and the fact that onshore winds generated by large-scale frontal systems fall predominantly within this vector field. Subsequent statistical evaluation of other vectors revealed that the north through east vector yielded the highest explained variance. The addition of wind strength and duration to the model did not add significantly to the variance explained.

Water temperature during drift

Once released from the beach gravel into the pelagic environment larval capelin are quickly and passively transported into offshore waters (Fortier and Leggett 1982; C. Taggart and W. C. Leggett, unpubl. data) where they feed and grow (Jacquaz et al. 1977). During the next few months they are largely restricted to the top 20 m of the water column (Jacquaz et al. 1977; Fortier and Leggett 1982, 1983).

Water temperatures used in the model are based on data recorded at station 27 (47°32′50″N, 52°35′10″W), 2 nautical miles (3.7 km) off Cape Spear near St. John's, Newfoundland (Akenhead 1983). This is the only northwest Atlantic hydrographic station for which a reliable, uninterrupted temperature time series is available (Akenhead et al. 1982). The Labrador current is the dominant hydrographic feature of the Newfoundland–Labrador area. Hence, temperatures recorded at station 27 reflect temperature trends in the area under consideration. This assumption is supported by our earlier finding (Frank and Leggett 1981b) that mean monthly sea surface temperatures varied less than 1°C over the range latitude 47–54°N during the period 1976–80. Furthermore, Poletayev (1979) has shown that by September the distribution of capelin larvae centers on the northern portion of the Grand Banks and, as a result, is in close proximity to the position of hydrographic station 27 during this phase of the life cycle (see Fig. 1). The exact form of the temperature variable, which is labelled TEMPSUM, was the sum of these monthly means (0–20 m) for the period July–December. This we have taken as an integrated measure of the thermal conditions experienced by larvae during larval drift and feeding. Winters (1983) employed a similar TEMPSUM index, also derived from station 27 data, to demonstrate the influence of annual temperature variability on the growth rates of sand lance (*Ammodytes dubius*) in the Grand Banks region.

Capelin abundance

Annual estimates of the abundance of 2-yr-old capelin for the 2J3K stock (Fig. 3) during the years 1970–78 are based on sequential cohort analysis. Abundances of the 1966–69 year-classes as 2-yr-olds were calculated from the estimates of the abundance of age groups 3–6 in 1972. This calculation used estimates of natural mortality rate and instantaneous spawning mortality identical to those employed in the sequential cohort analysis performed by Carscadden and Miller (1981). We assumed no fishing mortality in these years, since catches in 1966–69 averaged less than 2000 t as compared with 200 000 t during the mid-1970's.

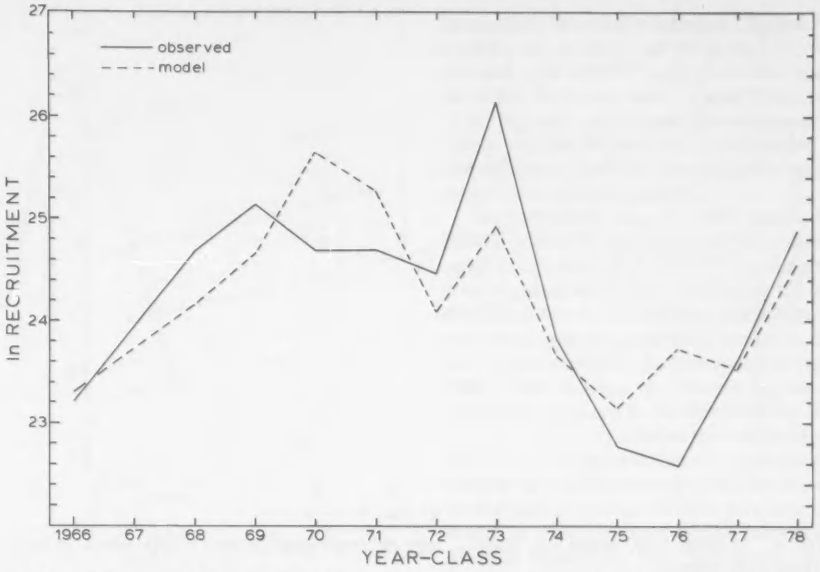

FIG. 3. Recruitment (1966–78 year-classes as 2-yr olds, from Carscadden and Miller 1981: table 7) and recruitment predicted from the model for Division 2J3K capelin stock.

Results and Discussion

The Model

Several forms of linear regression models incorporating the independent variables WIND and TEMPSUM were evaluated. In all models tested, year-class strength was transformed to natural logarithms (Hennemuth et al. 1980). The specific relationship yielding the highest explained variance between the natural logarithm of year-class strength (YCR) of 2-yr-old capelin, TEMPSUM, and WIND for the 2J3K stock was ln YCS = 16.10 − 0.19WIND + 0.19TEMPSUM ($R^2 = 0.58$, Table 1; Fig. 3). Data for 1967 were excluded from these analyses because the TEMPSUM value for this year deviated greatly from all other values in our time series. For the time series used in our analysis (1966–78) TEMPSUM values ranged from 42.40 to 51.18 except for 1967, which was 58.62. We examined a longer time series (33 yr) and found that 30 of the 33 values ranged from 39.01 to 53.38. Of the remaining TEMPSUM values, one was very low (1957 = 36.30) and two were high (1961 = 56.03 and 1967 = 58.62). Inclusion of the 1967 data greatly reduced the variance accounted for by the model (R^2 = 0.24). The sign of the regression coefficient for WIND was always negative, while that for TEMPSUM was always positive (Table 1). These trends are consistent with the demonstrated negative effect of increased wind interval on larval condition at emergence (survival) and the assumed positive influence of increased temperature on food availability to the larvae. Univariate analyses showed that the WIND and TEMPSUM variables were approximately equivalent in their contribution to explained variation in year-class strength (WIND, $r^2 = 0.38$; TEMPSUM, $r^2 = 0.43$).

The negative relationship between WIND and year-class strength suggests that strong year-classes are derived from the frequent release of discrete batches of good-condition larvae from the beach gravel. These batches of larvae are, in essence, cohorts that exhibit strong coherence in their time of formation

TABLE 1. Results of model relating recruitment (ln) to Division 2J3K capelin as 2-yr-olds to WIND and TEMPSUM (*$p < 0.05$).

Dependent variable: recruitment as 2-yr-olds (ln)

	df	Sum of squares	F value	r^2
Model	2	6.97	6.25	0.58*
Error	9	5.01		
Total	11	11.98		

Independent variables: WIND and TEMPSUM (Y-intercept = 16.098)

	Regression coefficient	t^a	SE	Partial r
WIND	−0.187	−1.78	0.1049	−0.51
TEMPSUM	0.194	2.09	0.0928	0.57

[a]The t values were derived to test the null hypothesis that the true value of the coefficient is equal to zero.

over large spatial scales in response to broad-scale onshore wind events. When relatively high water temperatures coincide with frequent releases, survival rate per cohort is expected to be high. This possibility is supported by the observation that the July and August mean monthly temperatures are more strongly correlated with TEMPSUM ($r^2 = 0.84$ and $r^2 = 0.73$, $n = 17$, respectively) than are the mean temperatures for other months (range of $r^2 = 0.32$–0.58). Substituting the July or August mean monthly temperature for TEMPSUM as an independent variable in the recruitment model did not, however, improve the fit of the model ($R^2 = 0.52$ and 0.39 for July and August, respectively).

This relationship between temperature and wind effects was further evaluated by running the model using a range of

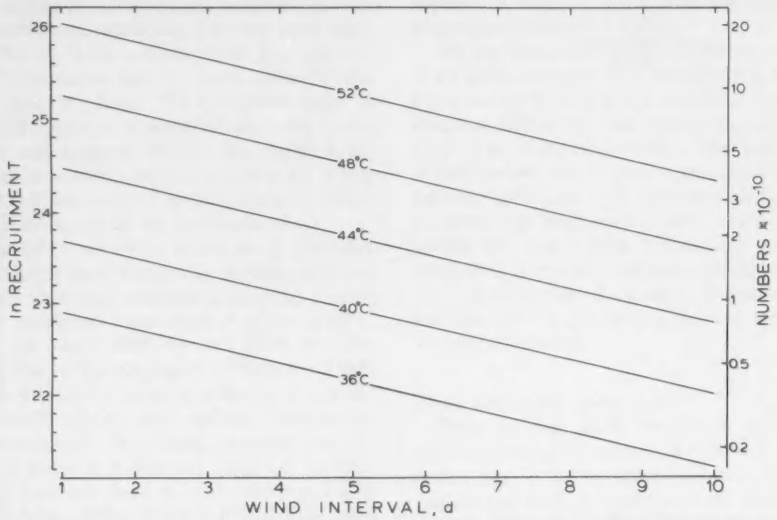

FIG. 4. Division 2J3K model run using a range of empirically derived WIND values at fixed TEMPSUM values.

empirically derived annual estimates for WIND and a range of fixed TEMPSUM values (Fig. 4). The analysis suggests that, given the range of temperatures and wind conditions experienced during the interval 1966–80, the length of the interval between onshore winds becomes progressively less critical to year-class formation as TEMPSUM increases.

The Biological Basis of Year-Class Variation

These analyses indicate that abiotic variables, specifically the frequency of onshore winds during the immediate posthatching period and water temperatures experienced during larval drift, are the most important ultimate regulators of year-class strength in capelin in eastern Newfoundland. In the 2J3K stock 58% of the year to year variation in year-class strength was accounted for by these two factors.

The most probable proximate cause of wind-related variation in year-class strength is deterioration in physical condition of larvae prior to emergence from the beach gravel. Yolk sac absorption is rapid, ranging from 3 to 8 d (mean 5.5) at the high- and mid-tide beach locations depending on temperature conditions (Frank and Leggett 1982a). Larval emergence is keyed to the occurrence of onshore winds, presumably because of survival advantages conveyed by increased food abundance and reduced predator densities created by the water mass exchange induced by such conditions (Frank and Leggett 1982b, 1983). When the interval between onshore winds exceeds that required for complete yolk sac absorption larval condition deteriorates rapidly (Frank and Leggett 1982a). If prolonged offshore wind conditions are coupled with high beach gravel temperatures, direct mortality prior to emergence may be high. This effect was apparently responsible for the four lowest levels of recruitment observed during the time series (1966, 1975–77) when the wind interval ranged from 5.5 to 10 d. Even under less severe conditions larval survival can be negatively influenced by wind interval. Frank and Leggett (1981a) found that the proportion of larvae in poor condition declines rapidly in samples taken progressively farther from the release site. This suggests that larvae weakened by prolonged beach residence are quickly lost from the population. Swimming ability is directly coupled to larval condition (Frank and Leggett 1982a). Depressed swimming ability can reduce both predator avoidance (Bams 1967; Lillelund and Lasker 1971; Theilacker and Lasker 1974; Hunter 1972) and feeding success (Laurence 1972; Rosenthal and Hempel 1970; Ware 1975). This may explain, in part, the higher loss rates of weakened larvae subsequent to emergence.

The evidence available also supports our working hypothesis that the proximate basis for the influence of TEMPSUM on year-class strength is the effect of water temperature on plankton production. As noted previously the Labrador Current dominates the hydrographic characteristics off eastern Newfoundland resulting in quite similar temperature conditions over large areas. We found TEMPSUM to be strongly correlated with cumulative growing degree-days at St. John's, Newfoundland, measured from April 1 to August 31 ($y = 11.32 + 0.40x$, $r = 0.86$, $n = 17$). We have previously documented a significant ($p < 0.01$) positive relationship between the biomass of zooplankton and growing degree-days (Frank and Leggett 1982b: table 2, fig. 7). During the interval 1964–81 cumulative growing degree-days (April 1–August 31) at St. John's varied from 660 to 1060. Applying these results to our earlier analysis (Frank and Leggett 1982b) indicates that this variation could result in an approximate 250% change (8.5–29.5 $mg \cdot m^{-3}$) in the biomass of zooplankton <250 μm, the principal prey of first feeding larvae, over the period in question. Enclosure experiments employing first feeding larvae indicate a strong positive relationship between larval growth rate (millimetres per day) and the biomass (milligrams per cubic metre) of zooplankton <250 μm ($y = 0.0337 \ln x - 0.0658$, $r^2 = 0.62$, $p < 0.01$; Frank and Leggett 1982b). The variation in edible zooplankton caused by annual differences in water temperatures could thus cause a variation of up to 100% in growth rate of first feeding larvae. The biomass of zooplankton >250 μm could vary up to 700% based on relationships between this size fraction and degree-days given in Frank and Leggett (1982b: table 2). This size fraction is presumably an important food component for later stage larvae and could similarly influence growth rates. The effect of such food variation on larval survival could be

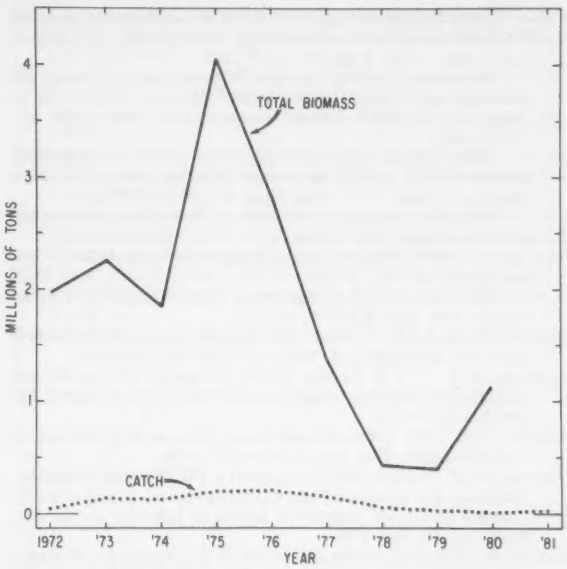

FIG. 5. Estimated total capelin biomass (age 2+, 1972–80, from Carscadden and Miller 1981) and annual catches (1972–81) for the Division 2J3K capelin stock.

direct or indirect. The occurrence of favorable food conditions has long been considered an important direct regulator of larval survival in fishes (Cushing 1975; Lasker 1975). In addition, larval growth rates have frequently been implicated in predator avoidance (Ware 1975; Marak 1960; Sysoeva and Degtereva 1965; Sherman and Honey 1971) and foraging ability (Rosenthal and Hempel 1970; Blaxter and Staines 1971; Hunter 1972). More recently, Policansky (1982) has shown that the onset of metamorphosis in flounders (*Platyichthyes stellatus*) is more strongly linked to size than age. If this is a general result, rapid growth under favorable feeding conditions may also operate to shorten the larval period, thereby increasing survival during the larval phase.

Recent Changes in Capelin Abundance — Over Exploitation or Recruitment Failure?

Sequential cohort analyses for the capelin stock occurring within NAFO Divisions 2J and 3K reveal a pronounced increase in total capelin biomass between 1974 and 1976 followed by a more dramatic decline between 1976 and 1979 (Fig. 5). It is only in the last decade that man has become a significant predator of capelin although capelin have been taken on and near the spawning beaches for generations. Prior to the 1950's, 20 000–25 000 t of capelin were taken annually in Newfoundland and Labrador for bait, fertilizer, and food for dog teams (Templeman 1968; Barnes 1974). During the early 1970's commercial exploitation of capelin by an international offshore fleet increased to approximately 200 000 t. The dramatic decline in total capelin biomass in 2J3K coincident with this increase in catch resulted from poor year-classes (FIg. 3), some of which were produced during the periods of relatively high capelin catches. This relationship implicated fishing as a major factor in the decline of the capelin stocks during the last half of the 1970's. However, total catch was small in relation to estimated total biomass throughout the period (FIg. 5). The results of our analysis argue against overfishing as the major factor in recent fluctuations in capelin biomass. Rather, recruitment failure resulting in a series of progressively weaker year-classes between 1974 and 1977 appears to have been a major contributor to the decline in total capelin biomass between 1977 and 1979. We believe the most probable cause of this recruitment failure was the occurrence of unfavorable meteorological and hydrographic conditions during and subsequent to larval emergence from the beach gravel.

The correlation (Y_{int} = 0.003, slope = 0.99, r = 0.76) betwen predicted and observed year-class strength for 2J3K capelin over the period 1966–78, in the absence of considerations of parent stock size, emphasizes the importance of factors relevant to the survival of individual fish at various key stages in their development to year-class formation. Such factors may, in fact, greatly outweigh the importance of parent stock size as the prime determinant of recruitment success. We believe a more systematic approach to the identification of these key stages in the early life history of other species could yield similar positive results. Of central importance is a quantitative knowledge of the variable(s) regulating survival during these "critical periods." With such knowledge reliable forecasts of future abundance should be possible given careful monitoring of relevant variables at appropriate time and space scales. The long-term inadequacy of several previously derived environmentally determined recruitment models (Gulland 1953, 1965; Bell and Pruder 1958) may result from their failure to conform to this scalar requirement. As a result they are unable to accommodate interannual or longer term shifts in the timing of important phenological events such as spawning times, development rates, and the timing of the initiation of drift which can significantly alter the timing of key responses to changing environmental conditions.

The approach we have described is not, however, without problems. The apparent precision in estimates of the timing of critical periods is subject to the compounding of errors due to the sequential dependency of empirical models used in their derivation. Such errors are no less important than those identified by Walters and Ludwig (1981) in the case of traditional recruitment models. Moreover, the errors in estimates of year-class size remain. For this reason the number of such sequential steps used to "time" the key developmental periods should be kept to a minimum and every effort should be made to minimize the unexplained variance in the intermediate level models employed. The major advantages of our approach are that the relevant parameters are easily measurable and that the model is open ended in the sense that greater complexity can be incorporated, if necessary, as additional key variables are identified without resorting to an entirely new model. This derives from the fact that the model is based on realistic biological mechanisms rather than a simple empirical fit to the data (Roff 1983).

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Environmental Controls of Marine Food Webs: Food Habits of Seabirds in the Eastern Chukchi Sea[1]

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Food habits of thick-billed murres (*Uria lomvia*), common murres (*U. aalge*), and black-legged kittiwakes (*Rissa tridactyla*) were examined at two breeding colonies in the eastern Chukchi Sea between 1976 and 1980. Cods (Gadidae), sculpins (Cottidae), sand lance (*Ammodytes hexapterus*), and capelin (*Mallotus villosus*) were the dominant (biomass) prey of thick-billed murres. Cods, sand lance, and capelin were the dominant prey of common murres and kittiwakes. Annual changes in the consumption of fishes by murres and kittiwakes suggest that available fish biomass in the eastern Chukchi Sea was low in 1976 and 1977, but increased each year through 1979 and 1980. The average size of several taxa of fishes eaten by the birds increased also between most years. Invertebrates were less important than fishes in all years, were eaten most frequently by thick-billed murres, and were eaten more frequently in 1976–77 than in 1978–79. A pattern of climatic cooling in the early 1970's followed by warming in the second half of the decade caused annual differences in the extent and duration of sea ice, and apparently in the spacial and temporal development of Alaskan Coastal Water, a major oceanographic feature of the Bering–Chukchi shelf. Fluctuations in the physical environment could have led to changes in fish populations through direct physiological and behavioral effects, or indirectly by altering the abundance of important zooplankton prey populations. Variability in the reproductive success of murres and kittiwakes in the northern Bering Sea and eastern Chukchi Sea corresponded with the apparent changes in fish stocks: reproductive success was very low in 1976 but improved in successive years. Short-term responses of seabirds to environmental fluctuation and its proposed effect on supporting food webs suggest that the stability of regional seabird populations could also be affected by long-term changes in weather and climate.

De 1976 à 1980, on a étudié les habitudes alimentaires de la marmette de Brünnich (*Uria lomvia*), de la marmette de Troïl (*Uria aalge*) et de la mouette tridactyle (*Rissa tridactyla*) dans deux colonies nicheuses de la mer de Chukchi orientale. Les morues (Gadidae), les chabots et chaboisseaux (Cottidae), le lançon d'Amérique (*Ammodytes hexapterus*) et le capelan (*Mallotus villosus*) représentaient les principales proies (en biomasse) de la marmette de Brünnich, tandis que la marmette de Troïl et la mouette tridactyle se nourrissaient plutôt de morues, de lançons d'Amérique et de capelans. Les variations annuelles de la consommation de poissons par les marmettes et la mouette indiquent que la biomasse disponible de poissons dans la mer de Chuckchi orientale était faible en 1976 et 1977, mais a augmenté chaque année jusqu'en 1979 et 1980. La taille moyenne de différentes espèces de poissons mangés par les oiseaux a aussi augmenté la plupart des années. Les invertébrés constituaient des proies moins importantes que les poissons pendant toutes les années et étaient consommés le plus souvent par la marmette de Brünnich, plus fréquemment en 1976–77 qu'en 1978–79. Un schème de refroidissement climatique au début des années 1970 puis un réchauffement au cours de la second partie de la décennie ont entraîné des différences annuelles au niveau de l'étendue et de la persistance de la glace de mer et apparemment du développement temporel et spatial du courant côtier d'Alaska, une importante caractéristique océanographique de la plate-forme Béring–Chukchi. Des fluctuations dans l'environnement physique peuvent avoir engendré des variations chez les populations de poissons et ce, à cause d'incidences physiologiques et comportementales directes ou, indirectement, d'importantes modifications de l'abondance des populations de zooplancton utilisé comme proie principale. Le succès variable de la reproduction des marmettes et de la mouette dans la mer de Béring septentionale et la mer de Chukchi orientale correspondait aux variations apparentes des stocks de poissons. Ainsi, le succès de la reproduction était

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tres faible en 1976 mais s'est amélioré les années suivantes. Les réactions à court terme des oiseaux marins aux fluctuations environnementales et l'incidence estimative de ces dernières sur les chaînes alimentaires pertinentes indiquent que la stabilité des populations régionales d'oiseaux marins pourrait aussi être touchée par des changements climatiques et météorologiques à long terme.

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Two breeding colonies in the eastern Chukchi Sea, Cape Thompson and Cape Lisburne, support about 500 000 piscivorous seabirds, of which approximately 90% are murres (*Uria* spp.) and 9% are black-legged kittiwakes (*Rissa tridactyla*) (Swartz 1966; Springer et al. 1984). In 1976 the reproductive success of the kittiwakes was extremely low at both colonies. Symptoms of the breeding failure were characteristic of season-long food shortage: few birds developed brood patches, copulation was seldom seen, few eggs were laid, egg laying occurred late in the breeding season, and most of the few chicks that hatched died, apparently of starvation. Reproductive success improved incrementally between 1977 and 1979 and remained relatively high in 1980 (Springer et al. 1984). The recovery was typified by progressively earlier laying dates, larger clutch and brood sizes, and fewer empty nests. Growth rates of kittiwake chicks were high in most years after 1976, indicating good late-season food availability in those summers.

These changes, and similar changes in the breeding biology of murres (Springer et al. 1984), signal variability of comparable magnitude in regional food webs. In this paper we show that the diets of murres and kittiwakes varied within breeding seasons and between years, variations that corresponded in time to differences in the reproductive performance of the birds and to interannual changes in water temperature and sea ice cover. We review recent and long-term climatic variability in northern Alaska and discuss possible interactions between climate, oceanography, and the fish populations supporting marine birds in the eastern Chukchi Sea.

Methods

Field work was conducted during portions of each summer of 1976–79 at Cape Thompson and 1976–80 at Cape Lisburne (Fig. 1). Except in 1976 at Cape Lisburne, murres and kittiwakes were collected at intervals during each breeding season as they returned to the colonies from offshore feeding areas. Most birds fed at considerable distances from both colonies and it was not practical to visit those areas to collect specimens. The stomach contents and the lining of the proventriculus of each bird were removed and stored in 70% ethanol within 2 h of collection. Food items were subsequently sorted and identified in the laboratory using appropriate taxonomic keys and preserved reference material.

Because food items were usually in an advanced stage of digestion when the birds returned to the colonies, invertebrate prey were often identified from parts such as rostra, jaws, uropoda, and eyes, and fishes were identified from otoliths. Sculpins (Cottidae) were counted and identified using preopercular bones as well as otoliths.

The sizes of most fish prey recovered from murres and kittiwakes were reconstructed from regressions of fish length on otolith length, and from fish weight on fish length (Table 1). Sculpins were often not identifiable to species or genera, and for analytical purposes regression equations for *Myoxocephalus quadricornis* were used to estimate their size. *Myoxocephalus quadricornis* was the only species of sculpin in the eastern Chukchi Sea for which size data were available.

Intact sand lance (*Ammodytes hexapterus*) and capelin (*Mallotus villosus*), from which otolith length–fish length regression equations were derived, were found on beaches near the colonies after storms or after they were dropped by birds. They were generally partially desiccated, making their wet weights unreliable. Based on the average weight and length of 14 relatively fresh sand lance (mean weight = 3.0 g, s = 1.9; mean length = 88 mm, s = 16) collected at Cape Lisburne in 1978, and the mean length of all colony/year samples, we estimated the average weight of individual sand lance consumed by seabirds by colony and year.

Most of the capelin collected by us were adult fish and were much larger than those taken by murres and kittiwakes. In 1978 at Cape Lisburne two specimens in the smaller size class were

FIG. 1. Map of the study area in northwestern Alaska.

TABLE 1. Regression equations for estimating lengths and weights of fish identified in prey remains of murres and kittiwakes.

Fish	Equation	Sample size	Correlation coefficient	Source
Arctic cod (*Boreogadus saida*)	Fish length (cm) = 2.198 × otolith length (mm) + 1.588	202	0.981	Frost and Lowry 1981
	log weight (g) = −5.196 + 3.031 log length (mm)	277	0.98	Craig et al. 1982
Saffron cod (*Eleginus gracilis*)	Otoliths > 8.5 mm			
	Fish length (cm) = 2.323 × otolith length (mm) − 4.839	110	0.963	Frost and Lowry 1981
	Otoliths ≤ 8.5 mm			
	Fish length (cm) = 1.740 × otolith length (mm) − 0.090	36	0.932	Frost and Lowry 1981
	log weight (g) = −5.610 + 3.233 log length (mm)	180	0.94	Craig and Haldorson 1981
Sculpins[a] (Cottidae)	Fish length (cm) = 4.009 × otolith length (mm) − 4.364			K. J. Frost and L. F. Lowry, unpubl. data
	log weight (g) = −6.016 + 3.46 log length (mm)	272	0.98	Craig and Haldorson 1981
Sand lance (*Ammodytes hexapterus*)	Fish length (mm) = 4.01 × otolith length (units)[b] + 19.0	31	0.91	This study
Capelin (*Mallotus villosus*)	Fish length (mm) = 3.42 × otolith length (units)[b] + 29.22	12	0.99	This study

[a]Equations were derived from specimens of *Myoxocephalus quadricornis*.
[b]12.5 units·mm^{-1}.

obtained (mean weight = 4.0 g, s = 3.0; mean length = 94 mm, s = 16). We used these values to estimate the average weight of individual capelin in each colony/year sample in the same way as for sand lance. The values (grams) we used for mean individual wet weights are as follows:

		Cape Lisburne	Cape Thompson
Sand lance	1977	3	2
	1978	3	3
	1979	3	4
	1980	4	—
Capelin	1977	—	2
	1979	2	3
	1980	3	—

Righteye flounders (Pleuronectidae) were generally young-of-year fish and were assigned an average weight of 1.0 g, based on the weight of one intact specimen. A variety of taxa, including snailfishes (Cyclopteridae, especially *Liparis* spp.), pricklebacks (Stichaeidae, especially *Stichaeus punctatus* and *Chirolophus* spp.), and herring (*Clupea harengus*), were categorized as "other fishes." They were generally small: the weight of three pricklebacks and one herring averaged 2 g each (s = 1.8).

Many otoliths were broken and could not be accurately measured even though they could be identified and the number of fish they represented could be determined. Therefore, weights of the various taxa of fishes in individual birds were estimated by multiplying the number of a given taxon in each bird by the average weight of all individuals of that taxon in that year. The average weight of a taxon was estimated by measuring a subsample of all intact otoliths and using the appropriate equations (Table 1), or was based on the above weight estimates.

Cod otoliths could not always be identified to species. In such cases the unidentified cod were apportioned to the two species (Arctic cod, *Boreogadus saida*, and saffron cod, *Eleginus gracilis*) according to the proportions of Arctic and saffron cod that were identified in all specimens collected in a given interval, e.g. 1–20 July 1977, Cape Lisburne.

Sand lance were aged by counting opaque and hyaline zones of otoliths (Reay 1972). Arctic cod, saffron cod, and sculpins were aged by comparing the calculated body lengths with length distributions of known aged fishes reported by Craig and Haldorson (1981). Capelin were aged on the basis of similar data provided by Pitt (1958a).

Intact invertebrates were measured and average weights were used to estimate weights of certain groups. The average weight of 13 amphipods (Amphipoda) was 0.2 g (s = 0.15 g); 10 mysids (*Neomysis* spp. and *Mysis* spp.) was 0.2 g (pooled sample); 20 euphausiids (*Thysanoessa* spp.) was 0.1 g (pooled sample); 17 shrimps (predominantly *Pandalus* spp. and *Eualus* spp.) was 0.5 g (s = 0.3 g); and 2 polychaetes (*Nereis* spp.) was 1 g (s = 0.2 g). "Other invertebrates," including hermit crabs (*Labidochirus splendescens*), squids (Cephalopoda), and snails (Gastropoda), were assigned an average weight of 1 g; no intact specimens in this group were recovered.

Information on murre and kittiwake feeding areas was obtained by land-based observations of directions taken by birds as they flew to and from the colonies, and by similar boat-based observations along the coastline up to 60 km from the colonies. In 1978 an aircraft was used to supplement the land- and boat-based observations during 25–29 July and 18–19 August. Transects were flown offshore up to 130 km from the colonies.

In analyzing differences in the lengths and biomass of fishes in seabird diets between colony/year samples, we first conducted Kruskal–Wallis tests. If the test result was significant ($P < 0.05$), we then used a multiple comparisons procedure (Conover 1980) to determine which samples differed from one another. We have used the notation K-W/MCP, $P < 0.05$ to indicate when these tests revealed significant differences between mean values.

Limitations

A general limitation of this study, and one common to most food habits studies, is the problem of accurately determining the number and size of prey organisms consumed by the birds. We collected birds as they returned to the colonies from feeding; however, differences between individuals in the time spent feeding and time since feeding are unknown. This problem is complicated by differential digestibility of fish and invertebrate

prey. Bradstreet (1980) concluded that the number of fish otoliths in murre stomachs provided a satisfactory index of the number of fishes recently ingested. Also, as we have done, he attempted to reduce bias by using invertebrate parts to estimate the number and size of the various taxa consumed by murres.

A related question is whether invertebrates found in bird stomachs were eaten by the birds directly, or indirectly after they were first eaten by fishes that subsequently became prey. With the exception of cumaceans, larval crustaceans, and copepods, we have assumed that all invertebrates in a bird stomach were intentionally consumed.

A specific limitation of this study is our use of weight estimates of sand lance, capelin, flatfishes, and "other fishes" based on small numbers of specimens. While the values we used can be improved upon with additional data, we applied the estimates in a uniform manner that should provide indices of the relative importance of these taxa in seabird diets within and between years. Likewise, the following data should provide indices for assessing other changes in diets, such as in the total biomass consumed, although the values we report probably underestimate the actual consumption when it is calculated on the basis of the energy requirements of seabirds (see Wiens and Scott 1975).

Results

Food Habits

The food habits of murres and kittiwakes during all years combined were similar at the two colonies (Tables 2 and 3) and were similar to those reported previously for Cape Thompson (Swartz 1966). A notable difference between the colonies was the near absence of mysids and euphausiids in diets at Cape Thompson. The two species of murres fed on similar kinds of fishes, although common murres (*Uria aalge*) took many fewer sculpins, flatfishes, and other fishes, but more sand lance and capelin, than did thick-billed murres (*U. lomvia*). Thick-billed murres took a greater number of invertebrates than did common murres. Kittiwakes rarely fed on sculpins or flatfishes, benthic taxa that would generally not be available to them because they feed only on prey that are at or near the surface. Polychaetes were taken more frequently by kittiwakes than by murres at both colonies, as were euphausiids at Cape Lisburne. Polychaetes are usually members of the benthic infauna, but they spawn in the water column (Johnson 1943) and the heteronereis worms become available to seabirds at that time. The apparently large contribution of amphipods to the diets of the kittiwakes at Cape Lisburne is misleading, since all but eight were recovered from a single bird.

Temporal Changes in Diets

Throughout the summer of 1976 at Cape Thompson, thick-billed murres fed almost entirely on cods, sculpins, and other fishes (Fig. 2), while common murres and kittiwakes fed on cods (Fig. 3). Sand lance were uncommon and capelin and flatfishes were absent in the birds' diets. Sand lance and capelin comprised an increasingly larger proportion of prey from one interval to the next in the summer of 1977, and they were important summer-long in 1979. The same pattern was apparent at Cape Lisburne (Fig. 2 and 3): sand lance and capelin became progressively more important in murre and kittiwake diets later in the summer of all years, and they became more important earlier in the summer in successive years. Flatfishes occurred in the diets of thick-billed murres only in 1978–79 at Cape Thompson and in 1979–80 at Cape Lisburne.

Besides the changes in the proportions of various fish taxa in seabird diets, there is an indication that the absolute quantity of prey in thick-billed murre diets also changed. With only one exception, both the number of fishes (Table 4) and the estimated biomass of those fishes (Table 5) in the diets of the birds from Cape Lisburne increased between years in each of the three intervals for which we have multiyear data. Although few of the differences were significant due to the large variability among birds in the amount of prey in their stomachs, there is the

TABLE 2. Occurrence of major taxa in diets of thick-billed murres (TBM), common murres (CM), and black-legged kittiwakes (BLK) at Cape Thompson, 1976–79. Values in parentheses represent the frequency among the total number of birds examined. Values not in parentheses represent the percent frequency, number, or weight, respectively, among birds with identifiable prey remains.

	TBM		CM		BLK	
	n	%	*n*	%	*n*	%
Number examined	246	(100)	62	(100)	116	(100)
Number empty	33	(13)	13	(21)	11	(9)
Frequency of invertebrates	115	54	6	12	20	19
Frequency of fish	182	85	45	92	91	87
A. Frequency of occurrence						
Cods	85	40	29	59	55	52
Sculpins	87	41	14	29	0	0
Sand lance	45	21	20	41	32	30
Capelin	26	12	12	24	17	16
Righteye flounders	19	9	3	6	0	0
Other fishes	28	13	3	6	3	3
Shrimps	69	32	3	6	4	4
Amphipods	29	14	3	6	0	0
Mysids	0	0	0	0	1	1
Euphausiids	1	<1	0	0	0	0
Polychaetes	18	8	0	0	12	11
Other invertebrates	36	17	1	2	7	7
B. Number of individuals						
Cods	350	8	203	26	241	27
Sculpins	835	25	137	17	0	0
Sand lance	213	6	271	34	325	36
Capelin	199	6	138	18	146	16
Righteye flounders	180	5	4	<1	0	0
Other fishes	271	8	16	2	6	<1
Shrimps	244	7	4	<1	34	4
Amphipods	910	27	12	2	0	0
Mysids	0	0	0	0	2	<1
Euphausiids	1	<1	0	0	0	0
Polychaetes	36	1	0	0	137	15
Other invertebrates	73	2	1	<1	14	2
C. Estimated wet weight (g)						
Cods	2574	43	2210	59	2626	63
Sculpins	1555	26	414	11	0	0
Sand lance	497	8	694	19	975	23
Capelin	595	10	383	10	415	10
Righteye flounders	180	3	4	<1	0	0
Other fishes	130	2	32	<1	12	<1
Shrimps	122	2	2	<1	17	<1
Amphipods	312	5	2.4	<1	0	0
Mysids	0	0	0	0	<1	<1
Euphausiids	<1	<1	0	0	0	0
Polychaetes	36	<1	0	0	137	3
Other invertebrates	73	1	1	<1	14	<1

TABLE 3. Occurrence of major taxa in diets of thick-billed murres (TBM), common murres (CM), and black-legged kittiwakes (BLK) at Cape Lisburne, 1977–80. Values in parentheses represent the frequency among the total number of birds examined. Values not in parentheses represent the percent frequency, number, or weight, respectively, among birds with identifiable prey remains.

	TBM		CM		BLK	
	n	%	*n*	%	*n*	%
Number examined	198	(100)	48	(100)	71	(100)
Number empty	16	(8)	3	(6)	4	(6)
Frequency of invertebrates	85	47	9	20	22	33
Frequency of fish	173	95	45	100	60	90
A. Frequency of occurrence						
Cods	99	54	35	78	28	42
Sculpins	89	49	10	22	4	6
Sand lance	75	41	25	56	29	43
Capelin	13	7	2	4	7	10
Righteye flounders	15	8	7	16	0	0
Other fishes	8	4	1	2	5	7
Shrimps	39	21	1	2	1	1
Amphipods	48	26	2	4	4	6
Mysids	19	10	3	7	0	0
Euphausiids	15	8	1	2	8	12
Polychaetes	12	7	0	0	13	19
Other invertebrates	11	6	1	2	2	3
B. Number of individuals						
Cods	660	13	202	31	158	5
Sculpins	529	10	17	3	5	<1
Sand lance	838	16	255	39	263	8
Capelin	55	1	60	9	29	<1
Righteye flounders	123	2	83	13	0	0
Other fishes	22	<1	6	<1	7	<1
Shrimps	165	3	5	<1	1	<1
Amphipods	985	19	4	<1	1318	42
Mysids	295	6	9	1	0	0
Euphausiids	1544	29	6	<1	1626	51
Polychaetes	8	<1	0	0	51	2
Other invertebrates	25	<1	3	<1	2	<1
C. Estimated wet weight (g)						
Cods	5028	51	1034	53	912	36
Sculpins	1135	12	18	1	30	1
Sand lance	2703	27	669	34	830	33
Capelin	132	1	122	6	87	3
Righteye flounders	123	1	83	4	0	0
Other fishes	44	<1	12	<1	14	<1
Shrimps	83	<1	2.5	<1	<1	<1
Amphipods	197	2	<1	<1	264	10
Mysids	59	<1	1.8	<1	0	0
Euphausiids	155	2	<1	<1	163	7
Polychaetes	8	<1	0	0	52	2
Other invertebrates	25	<1	3	<1	2	<1

appearance of a trend of increasing consumption of fishes in successive years. Such a trend is less apparent in the data from Cape Thompson except that fish numbers and biomass in 1976 were generally lower than they were in later years.

Invertebrates constituted a small proportion of prey biomass compared with that of fishes in the diets of all three species of birds. However, the apparent importance of invertebrates to thick-billed murres changed within and between years (Fig. 4). Invertebrates were least important in late summer of most years at both colonies, and they were less important summer-long in successive years. The decline in the consumption of invertebrates between years corresponded to the apparent trend of increasing consumption of fishes.

Characteristics of Prey Populations

The average size of most of the principal taxa of fishes eaten by murres and kittiwakes in the eastern Chukchi Sea increased between most years (Fig. 5). Although the annual contribution of various age classes to the total take of individual taxa undoubtedly changed, many of the differences between years apparently can be accounted for by changes in size-at-age of the fishes.

The average length of sand lance was longer each successive year between 1977 and 1980 at both colonies (K-W/MCP, $P < 0.05$). Capelin were larger in 1979 than in 1977 at Cape Thompson and were larger in 1980 than in 1979 at Cape Lisburne (K-W/MCP, $P < 0.05$). Most sand lance were age class 1+, with a few age class 0+ individuals; sand lance older than age class 1+ were uncommon except at Cape Lisburne in 1977 when age class 2+ fish accounted for an unusual bimodal size distribution that year. Andriyashev (1954) noted that sand lance in the coastal zone of Murmansk also were predominantly age class 1+. Capelin were predominantly age class 1+ juveniles, although remains of a few larger adults were recovered. The adult capelin were spawning as shown by developing reproductive products in both males and females.

Arctic cod at Cape Lisburne exhibited the same trend of increasing average size in later years, and the differences between 1977–78 and 1978–79 were significant (K-W/MCP, $P < 0.05$). Size distributions of Arctic cod tended to be bimodal: smaller fish were predominantly age class 1 and larger fish were predominantly age class 3. The annual increases in average size of Arctic cod at Cape Lisburne resulted from changes in relative numbers of the two age classes between years, as well as from apparent annual increases in average sizes of age class 1 fish. Craig and Haldorson (1981) reported that the sizes of age classes 1–5 Arctic cod in Simpson Lagoon (northeast of Cape Lisburne in the Beaufort Sea) were all larger in 1978 than in 1977, and the difference was significant for age class 2 fish, which averaged 15 mm longer in 1978 ($P < 0.001$). At Cape Thompson the average size of Arctic cod decreased between 1976 and 1977 because of a large change in proportions of age classes. However, the average sizes of individual age classes appeared to increase between years, especially between 1977 and 1979, as they did at Cape Lisburne and Simpson Lagoon.

The majority of sculpins in all years were age classes 0–2, and the average length increased between most years at both Cape Thompson and Cape Lisburne. The increases were significant between 1976 and 1977 at Cape Thompson and between 1978 and 1980 at Cape Lisburne (K-W/MCP, $P < 0.05$).

Saffron cod were considerably smaller than Arctic cod (Fig. 5), and most were age class 0 fish with a few age class 1 fish. Unlike the other species, saffron cod were smaller in successive years at both colonies, except between 1978 and 1979 at Cape Thompson (K-W/MCP, $P < 0.05$). A change in age class strength probably explains the difference in size of saffron cod between 1978 and 1979 at Cape Thompson.

The sizes of sand lance, capelin, sculpins, and Arctic cod tended to increase with decreasing latitude. Within all years that samples were collected at both Cape Thompson and Cape Lisburne, sculpins and capelin were always significantly larger at Cape Thomspon. Sand lance also tended to be larger at Cape Thompson than at Cape Lisburne, significantly so in 1979.

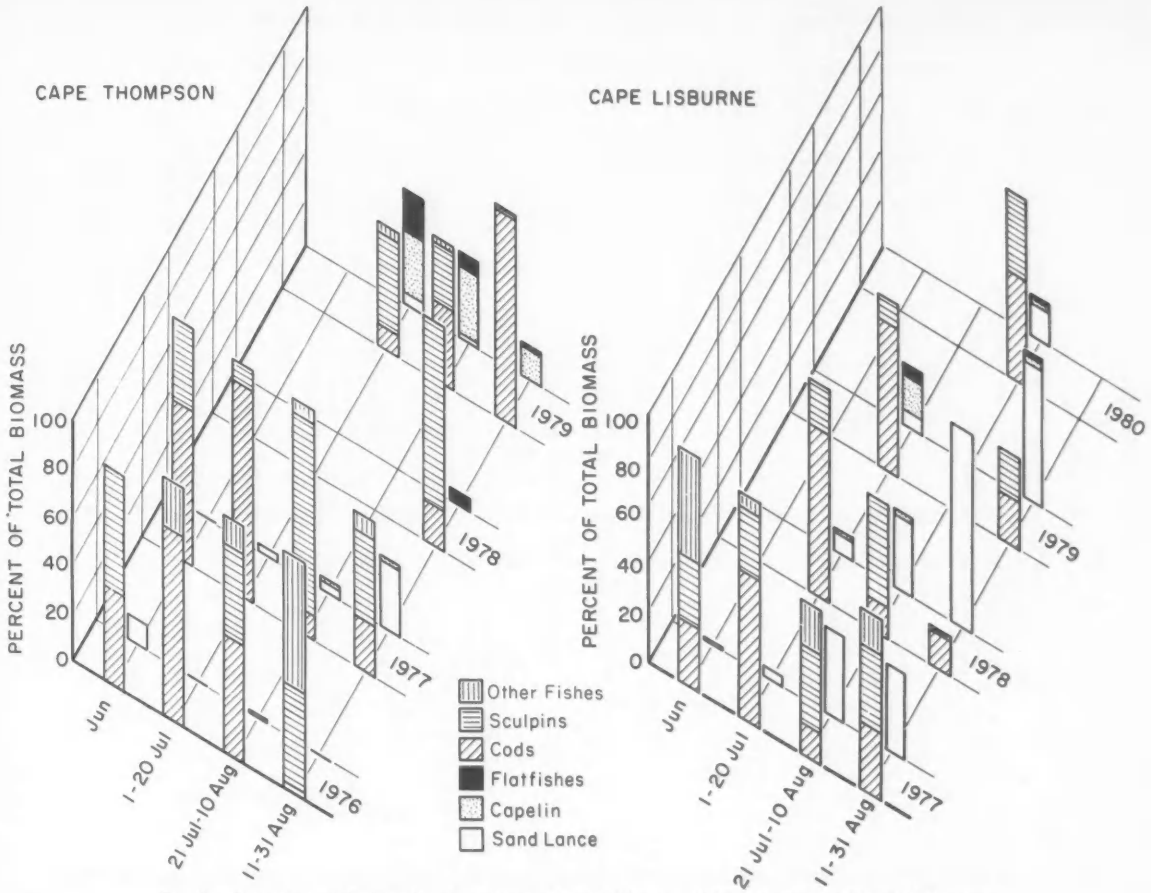


FIG. 2. Percent contribution of various taxa to the total biomass of fishes in diets of thick-billed murres.

Arctic cod were significantly larger at Cape Thompson than at Cape Lisburne in 1977. Increasing size with decreasing latitude has been reported by Andriyashev (1954) for sand lance in the Barents Sea, and by Lowry and Frost (1981), who showed that Arctic cod in the Bering Sea were larger than in the Chukchi and Beaufort seas. In contrast, saffron cod tended to be larger at Cape Lisburne than at Cape Thompson. Wolotira et al. (1979) found a similar north to south decline in size-at-age of saffron cod in the Bering and Chukchi seas in 1976.

Feeding Areas

The majority of murres from Cape Thomspon fed south of the colony in all years during June and most of July. In 1976, flight directions shifted somewhat to the west in August, but few murres were ever seen flying north. A clear shift to the north occurred in late July of 1977 and by early August nearly all murres from Cape Thompson fed north of the colony. A similar shift occurred in 1978, although there was somewhat less distinction between early and late season feeding areas. We observed few murres during aerial surveys offshore of Cape Thompson in 1978 and there was no obvious pattern of distribution at sea. In 1979, murres fed over a broader area throughout the summer than during previous years; flight directions were widely scattered between south and west in early July. About half of the murres shifted to the west and north by early August, and thereafter murres could be seen flying to and from nearly all offshore directions.

Few murres were seen on the water between Cape Thompson and Cape Lisburne, except in the immediate vicinity of a colony at Cape Lewis, during any of our aerial surveys or during numerous flights we made when going between field camps. Therefore, when murres from Cape Thompson fed north of the colony, they probably mingled with birds from Cape Lisburne. In August of 1978 we intercepted several flocks of southbound murres west of Cape Lisburne and followed them to Point Hope in our survey aircraft. At Point Hope we watched other flocks arriving from the same direction and subsequently confirmed that they were returning to Cape Thompson.

Murres at Cape Lisburne fed northeast of the colony in Ledyard Bay during June and most of July in 1977–79. By early August they foraged generally north of the colony, and gradually shifted more to the northwest by late August. Early-season observations were not made in 1976; however, in late August murres were flying in directions farther to the west than in any subsequent year. Observations made during aerial transects flown in July 1978 indicated that murres were feeding nearshore and in the center of Ledyard Bay near the interface of two water masses.

Kittiwake feeding areas tended to be closer to the colonies, but generally lay in the same direction as those of murres in June

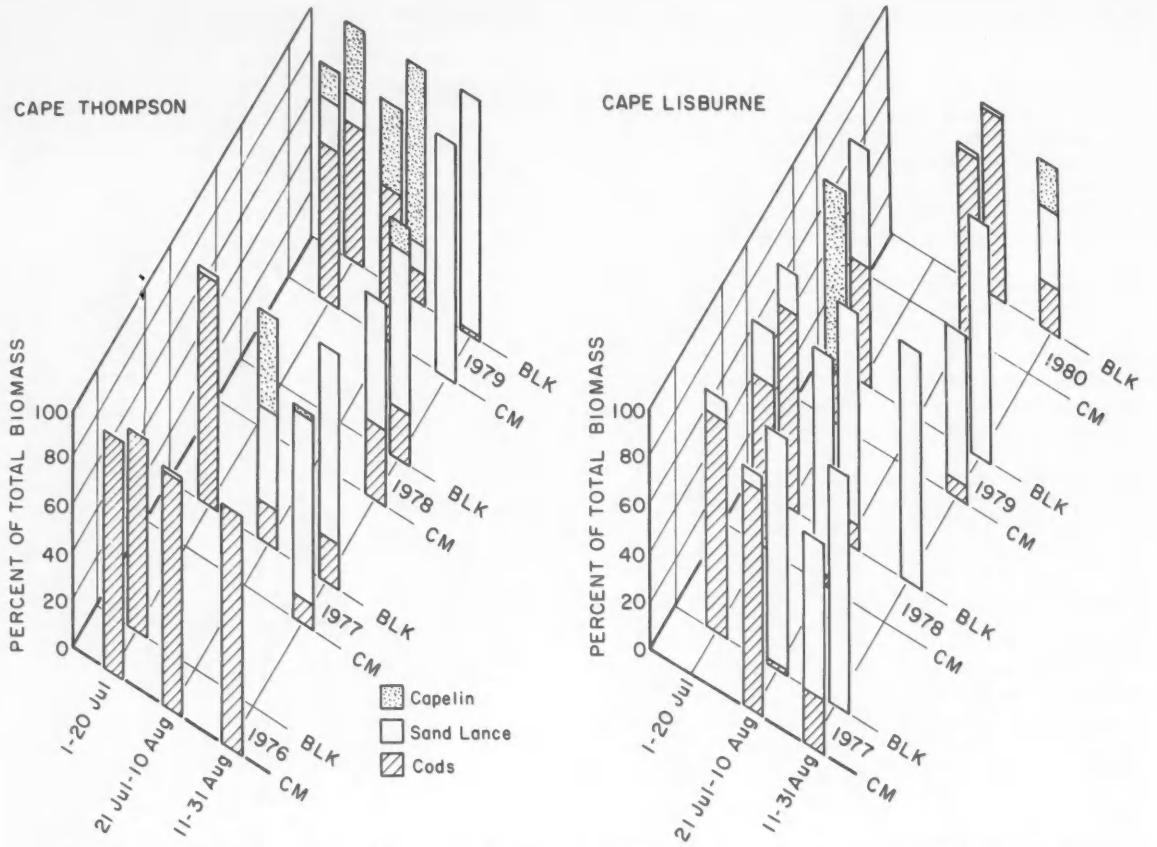


FIG. 3. Percent contribution of various taxa to the total biomass of fishes in diets of common murres and black-legged kittiwakes.

and July. Beginning sometime between mid-July and early August of all years except 1976, kittiwakes concentrated along the coastline north and south of Cape Thompson and east of Cape Lisburne. The shift to coastal feeding occurred when sand lance or capelin arrived near shore east of Cape Lisburne and north of Cape Thompson, and it occurred earlier in the summer in later years. In 1976 when sand lance and capelin were absent, kittiwakes foraged widely offshore throughout the summer.

Discussion

The patterns of change in the diets of murres and kittiwakes at Cape Thompson and Cape Lisburne between 1976 and 1980, i.e. an apparent increase in fish biomass in diets of thick-billed murres corresponding to a decrease in the importance of invertebrates and an increase in the proportions of sand lance and capelin in diets of murres and kittiwakes, are consistent with the hypothesis that the availability of fish biomass to seabirds in the eastern Chukchi Sea was relatively low in 1976, but increased in successive years. The annual increases in the average size of several of the fish taxa support this view and suggest that differences in fish availability between years could have been related to environmental conditions that affect fish growth, reproduction, and distribution. Sea ice and seawater temperature, important elements of the highly variable environment of northern Alaska, fluctuated considerably during the past decade and the fluctuations could have caused changes in regional food webs and hence in seabird breeding biology.

Regional Physical Processes

The southern extent of winter ice in the Bering Sea characteristically varies considerably between years, a consequence of changing weather patterns (Walsh and Johnson 1979; Johnson 1980; Niebauer 1980). Beginning in 1973, anomalous atmospheric circulation resulted in the progressive cooling of the Bering Sea and led to large negative deviations from normal sea-surface temperature and shelf bottom water temperature and a large positive deviation from normal ice cover by 1976 (Dickson and Namias 1979; Niebauer 1980). Between fall 1976 and spring 1979 the trend reversed: sea-surface temperature, which was 1.4°C below normal in 1975, rose 0.7–0.8°C·yr^{-1}. Sea ice, which reached its maximum southern extent in the winter of 1975–76, decreased about 10%·yr^{-1} from 1977 through 1979 (Niebauer 1980). Annual changes in ice cover and sea-surface temperatures were not confined to the Bering Sea, but were also pronounced in the eastern Chukchi Sea (Fig. 6).

Besides sea ice, the eastern Chukchi Sea is dominated year-round by a strong barotropic current flowing north out of the Bering Sea (Coachman et al. 1975; Coachman and Aagaard 1981). Water velocity of 150 cm·s^{-1} through Bering Strait is common and mean volume transport is in the order of 1×10^6 to

TABLE 4. Numbers of fishes in diets of thick-billed murres (arithmetic mean number per bird). nd = no data.

	June			1–20 July			21 July–10 Aug.			11–31 Aug.		
	n	$\bar{x}$	*s*	*n*	$\bar{x}$	*s*	*n*	$\bar{x}$	*s*	*n*	$\bar{x}$	*s*
Cape Thompson												
1976	11	1.2	0.6	8	1.4[a]	1.4	15	1.1[b]	1.6	11	6.4	11
1977	32	1	2.6	9	6.4	8.1	20	25	54	45	8.7	14
1978		nd			nd			nd		14	10	15
1979		nd		26	15	3.7	34	7	8	8	7	7
Cape Lisburne												
1977	6	5	7	22	5.6	7.8	15	6.6	8.7	9	9	12
1978		nd		17	8	14	29	20[c]	20	10	15	13
1979		nd		17	12	14		nd		19	23	25
1980		nd			nd		32	6.2	8.4		nd	

[a]Value is less than in 1–20 July 1979 (K-W/MCP, $P < 0.05$).
[b]Value is less than in 21 July–10 Aug. 1977 and 1979.
[c]Value is greater than in 21 July–10 Aug. 1977 and 1980.

TABLE 5. Weight of fishes in diets of thick-billed murres (arithmetic mean weight (g) per bird). nd = no data.

	June			1–20 July			21 July–10 Aug.			11–31 Aug.		
	n	$\bar{x}$	*s*	*n*	$\bar{x}$	*s*	*n*	$\bar{x}$	*s*	*n*	$\bar{x}$	*s*
Cape Thompson												
1976	11	11	17	8	34	40	15	15[a]	28	11	11	21
1977	32	3.8	8.3	9	44	54	20	30	32	45	18	30
1978		nd			nd			nd		14	17	16
1979		nd		26	24	29	34	25	26	8	61[b]	66
Cape Lisburne												
1977	6	10	13	22	19[c]	29	15	14[d]	18	9	23	36
1978		nd		17	23	44	29	43	70	10	53	55
1979		nd		17	64	81		nd		19	57	67
1980		nd			nd		32	54	84		nd	

[a]Value is less than in 21 July–10 Aug. 1977 and 1979 (K-W/MCP, $P < 0.05$).
[b]Value is greater than in 11–31 Aug. 1976–1978.
[c]Value is less than in 1–20 July 1979.
[d]Value is less than in 21 July–10 Aug. 1978 and 1980.

2×10^6 $m^3 \cdot s^{-1}$. In summer the total flow is composed of three distinct water masses, Anadyr Water, Bering Shelf Water, and Alaskan Coastal Water, as defined by three temperature–salinity envelopes. Anadyr Water and Bering Shelf Water, which originate at depth off the continental shelf of the Bering Sea, are cold, high-salinity water masses. Alaskan Coastal Water, in contrast, is a warm, low-salinity water mass found in the northeastern Bering and eastern Chukchi seas. Alaskan Coastal Water tends to follow the 40-m isobath north of Bering Strait, which takes it eastward toward the Cape Thompson–Point Hope region. North of Point Hope the current tends to follow the Alaskan coast, flowing northeast around Cape Lisburne and into the Beaufort Sea east of Barrow (Fleming and Heggarty 1966; Hufford 1973; Coachman et al. 1975).

Alaskan Coastal Water develops annually on the shallow shelf of the northeastern Bering Sea (Fig. 7) from cold, relatively saline water that is diluted by melting ice and river input, primarily from the Yukon River, and rapidly heated by insolation (Coachman et al. 1975). The temperature of coastal water flowing through Bering Strait may rise from near 0 to 10°C during the first month following dissipation of sea ice (Bloom 1964; Ingraham 1981). The seasonal development of the Alaskan Coastal Water mass, therefore, apparently depends on the winter extent of ice into the Bering Sea and its rate of retreat in spring.

Seabird Food Webs

The Bering Sea shelf shoreward of about the 100-m isobath has high levels of primary productivity, about 166 g $C \cdot m^{-2} \cdot yr^{-1}$ (Walsh and McRoy 1983). Poor coupling to pelagic herbivores, however, results in a relatively inefficient system, with a major fraction of the annual production being lost to endemic pelagic food webs (Cooney and Coyle 1982). High nitrate concentrations in Anadyr and Bering Shelf waters (Husby and Hufford 1969; Sambrotto et al., in prep.) promote primary production rates as high as 4 g $C \cdot m^{-2} \cdot d^{-1}$, rates comparable to those in the major upwelling areas of the world (McRoy et al. 1972). The only limitation to the total yearly phytoplankton growth in the western strait area appears to be the length of time suitable water

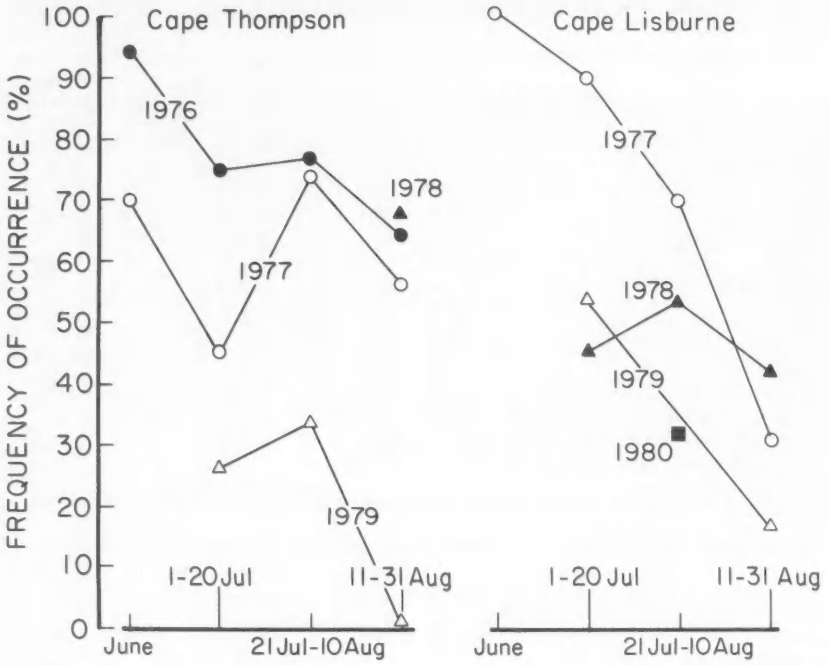


FIG. 4. Frequency of occurrence of invertebrates in diets of individual thick-billed murres.

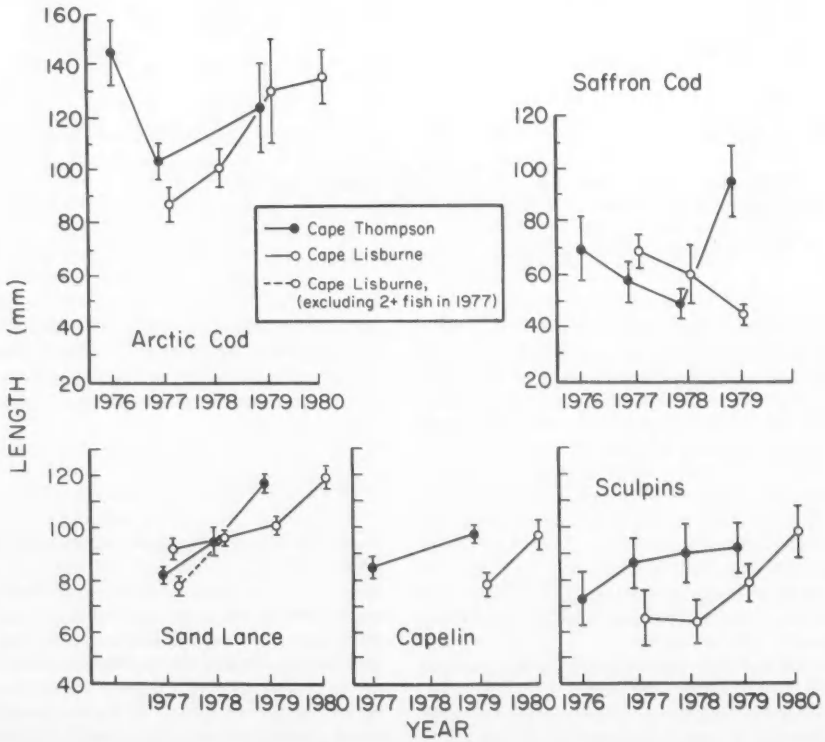


FIG. 5. Average length of fishes eaten by murres and kittiwakes in the eastern Chukchi Sea. Bars indicate the 95% confidence interval.

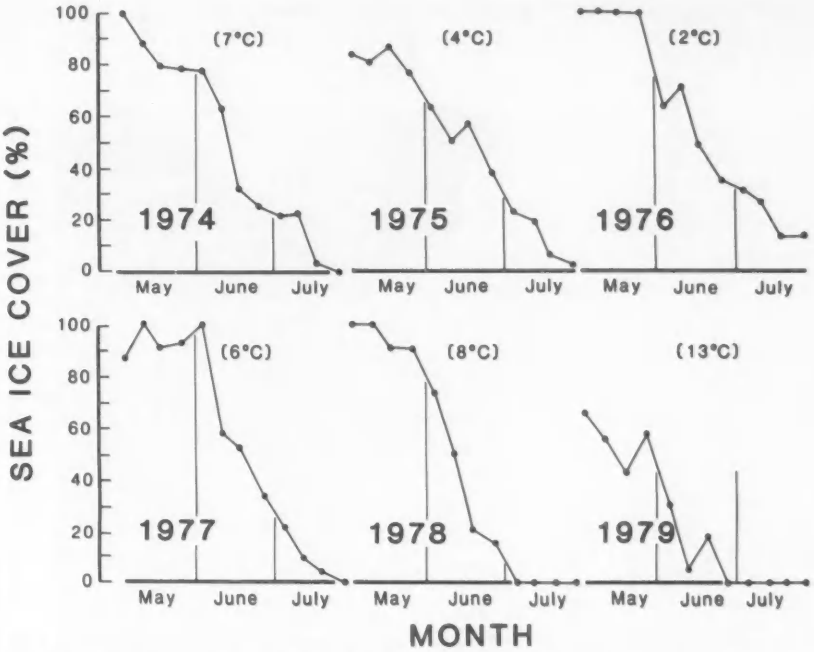


FIG. 6. Percent ice cover over the northern Bering Sea and eastern Chukchi Sea. Numbers in parentheses are sea-surface temperatures measured near Cape Lisburne (mean date = 16 July, s = 3 d). Water temperatures were measured directly or from infrared imagery.

column light conditions prevail, an interval determined by the day length, the angle of the sun, and the duration of seasonal sea ice.

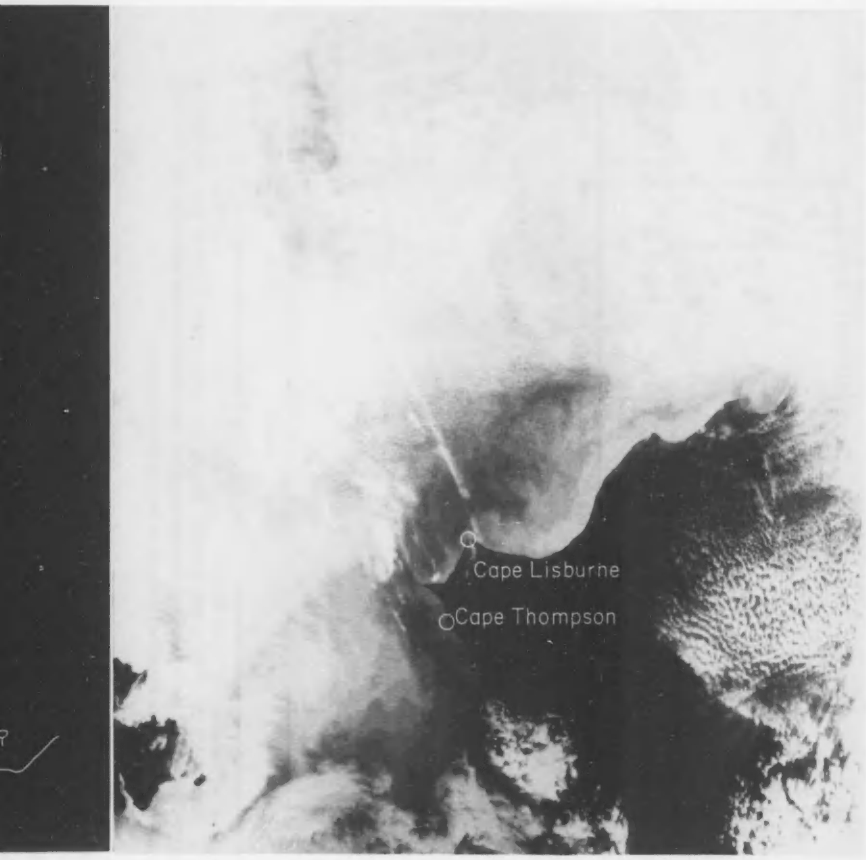
Because of the volume and speed of water transported through Bering Strait, a significant portion of the carbon fixed there during summer is swept downstream. Stoker (1981) suggested that such a process would explain high standing stocks of predominantly boreal Pacific benthic invertebrate macrofauna in the southern Chukchi Sea. Particulate organic matter advected from the northern Bering Sea shelf, plus that originating in Bering Strait, probably contributes significantly to the annual carbon budget of the Chukchi Sea.

The flow of water from the Bering Sea also plays an important role in determining the composition and abundance of zooplankton assemblages in Bering Strait and in the eastern Chukchi Sea. Endemic Bering Sea copepods, including *Eucalanus bungii*, *Calanus cristatus*, *C. plumchrus*, *Acartia longiremis*, and *A. clausi*, are advected into the eastern Chukchi Sea during summer, and contribute significantly to diversity and standing stocks of zooplankton in nearshore waters (Johnson 1956; Redburn 1974). The intrusion of warm Alaskan Coastal Water creates a temperature regime favorable for the rapid development and high production of meroplankton, particularly barnacle larvae, and as a result zooplankton biomass in the warmer coastal zone during summer is about an order of magnitude higher than in the colder central Arctic Ocean (Redburn 1974).

Sand lance are seasonal predators of the nearshore zooplankters and are considered a coastal, shallow-water species except in winter when they move into deeper water and spawn (Andriyashev 1954; Macy et al., National Marine Fisheries Service, NOAA, Seattle, WA, unpubl. data; Rogers et al. 1979). Shoaling year class 1+ fish run onshore in summer in northern Alaska (pers. obs.) and in the Barents Sea (Andriyashev 1954), presumably in response to the abundance of prey. Sand lance in the eastern Chukchi Sea feed on the copepods *C. plumchrus*, *Pseudocalanus* spp., *Acartia* spp., and *Oithona* spp., on the cladocerans *Podon* spp. and *Evadna* spp., and on larval euphausiids and juvenile bivalves (Springer et al., unpubl. data). In the Barents Sea, sand lance feed on *Calanus finmarchicus*, meroplanktonic forms of barnacles and larvae of euphausiids and amphipods during early summer, and shift to small copepods, particularly *Microsetella* spp., *Acartia* spp., and *Oithona* spp., towards late summer (Andriyashev 1954). Sand lance in the northern Gulf of Alaska feed predominantly on calanoid copepods and barnacle larvae (Rogers et al. 1979; Blackburn et al. 1981). The abundance of *A. clausi*, the numerically dominant zooplankter in Norton Sound, is directly correlated with warming water temperature (Niemark 1979), and temporal patterns of distribution of barnacle larvae in the eastern Chukchi Sea near Barrow, Alaska, are strongly influenced by the dynamic hydrographic regime imposed by the seasonal intrusion of Alaskan Coastal Water (Redburn 1974). Therefore, the occurrence of sand lance earlier in the summer each year after 1976 and concurrent increases in their abundance could have been functions of the rate of development of prey populations, a rate that apparently depends on the pattern of warming in the coastal zone.

Smaller average sizes of sand lance in colder years in the eastern Chukchi Sea, as reported for sand lance on the Grand Bank (Winters 1981), could have resulted from poor coupling to seasonal prey because of delayed development of prey populations. Also, sand lance size might be influenced directly by the effect of water temperature on the fish. For example, the

FIG. 7. Alaskan Coastal Water development. NOAA 4 infrared imagery with a temperatur
from Norton Sound and the Yukon River intrudes into the ice-covered Chukchi Sea. Right: 2
Sea past Cape Lisburne.



nperature enhancement scale of −3 to 12°C. Left: 7 June 1980. Warm Alaskan Coastal Water (darker shading)
Right: 29 July 1980. With the dissipation of the sea ice, the warm coastal jet flows through the eastern Chukchi

emergence of sand lance (*A. marinus*) in spring from the sand where they overwinter is related to warming water temperatures (Winslade 1974), and the incubation time of sand lance eggs increases from 13 d at 16°C to 33 d at 6°C (Inoue et al. 1967). Delays in emergence dates and prolonged incubation times of eggs in colder years could shorten the growing season for sand lance and aggrevate the effects of relatively low prey availability.

Annual differences in seasonal water temperatures in the eastern Chukchi Sea could likewise account for the annual differences in abundance and size of capelin. Pitt (1958b) reported that capelin on the Grand Bank will spawn in a rather broad range of water temperatures, but spawning and embryonic development is delayed in colder years. Although adult capelin do not feed while spawning, juveniles feed intensively throughout the summer, predominantly on copepods (Vesin et al. 1981). Therefore, the presence or absence of juvenile capelin near Cape Thompson and Cape Lisburne in summer could be related to the presence or absence of seasonally abundant food, as proposed in the case of sand lance. Pitt (1958a) also showed that growth rates of capelin were slower in colder years than in warmer years and suggested that the difference was a factor of water temperature and food conditions.

The most abundant and widespread fishes in the eastern Chukchi Sea are Arctic cod and sculpins (Alverson and Wilimovsky 1966; Craig and Haldorson 1981; Craig et al. 1982). Arctic cod feed on copepods, amphipods, and mysids (Lowry and Frost 1981; Craig et al. 1982). Small sculpins feed mainly on mysids, amphipods, and isopods (Craig and Haldorson 1981). The degree to which these food webs might be affected by seasonal warming patterns or subsidized by particulate carbon imported from the Bering Sea is unknown. If there is a positive effect, then it should be greater in warmer years when the annual production cycle begins relatively early in summer, and it should be greatest near Bering Strait where the particulate load would be highest. Increasing sizes of Arctic cod and sculpins between 1976 and 1980, and from north to south, suggest such effects.

Unlike other fishes, saffron cod apparently decreased in size from 1976 to 1978 at Cape Thompson and from 1977 to 1979 at Cape Lisburne, in spite of improving environmental conditions. Saffron cod are found in greatest numbers in summer in the northern Bering Sea and southern Chukchi Sea (Lowry and Frost 1981) and are the most abundant species in Norton Sound (Wolotira et al. 1979). Saffron cod are also found along the coast of the Beaufort Sea as far east as the Mackenzie Delta and Tuktoyaktuk Peninsula, but are not generally numerous (Craig and Haldorson 1981). They were the more common of the two species of cods taken by the birds in late summer in the eastern Chukchi Sea, comprising 67% of 312 individual cods identified to the species level in the 11–31 August interval of all years combined. In contrast, Arctic cod comprised 84% of 391 cods in the combined intervals from June to 10 August.

Neimark (1979) found that 80% of the diet of saffron cod in Norton Sound consisted of copepods and 20% consisted of cladocerans. Copepods and cladocerans are also important food of sand lance and capelin, and because sand lance, capelin, and saffron cod are all found nearshore in summer, competition among them for prey could occur. Vesin et al. (1981) suggested that declines in numbers of capelin in the northeast Newfoundland–Labrador area could have increased copepod availability sufficiently to influence growth and development of other zooplankton consumers. They cited recent dramatic increases in the abundance of Arctic cod and short-finned squid (*Illex illecebrosus*) as evidence of such a relationship. In the eastern Chukchi Sea, the numbers and sizes of capelin and sand lance increased during the years that saffron cod declined in size, suggesting similar competitive interactions among these coastal zooplanktivores.

Finally, the absence of flatfishes in the diets of thick-billed murres in the earlier, colder years of this study also could have been a function of water temperature. Pruter and Alverson (1962) believe that the spawning of *Hippoglossoides robustus* and *Limanda aspera*, the two most abundant pleuronectids in the Chukchi Sea, is generally unsuccessful because of the harsh temperatures offshore and because the coastal jet would sweep the pelagic eggs and larvae north into an even more severe environment. They suggested that the presence of these two species of flatfishes in the Chukchi Sea depends instead on the transport of eggs, larvae, and juveniles from the Bering Sea. The abundance of flatfishes, which is very low throughout the Chukchi Sea compared with the Bering Sea (Pruter and Alverson 1962), could be expected to be greater in warmer years, however, when the Alaskan Coastal Water mass develops early in the summer.

Biology of Murres and Kittiwakes

Summer foraging patterns of murres and kittiwakes and differences in those patterns between years could have been related to changes in the physical environment and the effects we suggest these changes had on food webs and prey availability. The case of kittiwakes appears relatively simple. During early summer of all years, kittiwakes foraged widely offshore. When sand lance or capelin arrived nearshore, kittiwakes shifted their feeding accordingly. The shift occurred between early July and mid-August, depending on the year; it was earlier in warmer years and later in colder years. In the very cold summer of 1976 when neither sand lance nor capelin were present, kittiwakes fed offshore throughout the summer.

Changes in murre foraging areas during the summer and between years are not as straightforward as those of kittiwakes. In June and early July of all years, murres from Cape Thompson fed south of the colony toward Bering Strait where energy levels are higher than in the Chukchi Sea. However, zooplankton, for example copepods, which are abundant in the northern Bering Sea and Bering Strait region as eggs, nauplii, and copepodids in early summer, are carried north into the eastern Chukchi Sea. The northward movement of an assemblage of organisms, including zooplankton and their fish predators, could lead to the shift in murre feeding areas at Cape Thompson from south to west to north during summer. By mid-August of most years, the center of murre prey abundance appeared to be situated north and west of Cape Lisburne, since large numbers of murres from both colonies fed there. Wing (1974) showed that copepod biomass and diversity in the eastern Chukchi Sea were greatest in a region of relatively warm water northwest of Cape Lisburne in September–October 1970. The occurrence of a variety of fish species was also higher there at that time than in the surrounding waters (Ingham et al. 1972). Annual variations in foraging patterns of murres at Cape Thompson could be explained by differences in the timing of annual production cycles in the northern Bering Sea–Bering Strait region, and consequently the timing and rate of export of food web organisms.

The feeding distribution of murres offshore of Cape Lisburne in July 1978 coincided with the position of a frontal zone

between warm Alaskan Coastal Water and cold Arctic Ocean water. Such fronts often have significant biological effects by mechanically concentrating organisms and enhancing productivity (Owen 1981). A front between Alaskan Coastal Water and Arctic Ocean water is apparently a regular physical feature in summer that could account for the regular use of Ledyard Bay by feeding seabirds. The position of the front might vary depending on the season and the year, explaining the variability of feeding patterns of murres from the Cape Lisburne colony.

Changes in the breeding biology of murres and kittiwakes between 1976 and 1980 and the corresponding changes in prey populations represent adjustments to the large-scale environmental fluctuations that occurred during that period. Although we lack many details, effects of the climatic oscillation during the 1970's were apparently manifested in at least two different food webs: arctic benthic and demersal food webs that include Arctic cod, sculpins, and flatfishes and boreal pelagic food webs that include sand lance and capelin. Furthermore, environmental effects on seabirds and their food webs in northern Alaska were not restricted to Cape Thompson and Cape Lisburne. The same pattern of breeding failure followed by recovery in kittiwakes and common murres at Bluff in Norton Sound was documented between 1975 and 1980 (Drury et al. 1981; Springer et al. 1984). Food availability at Bluff also seemed to be the most important factor in determining annual levels of reproductive success. Apparent food shortages likewise led to a poor breeding season for murres and kittiwakes on St. Lawrence Island in 1976 (Searing 1977). Murres and kittiwakes in Norton Sound feed primarily on sand lance and saffron cod, and on St. Lawrence Island they feed on cods, sand lance, and capelin (Springer et al., unpubl. data). St. Lawrence Island and Norton Sound are located in the headwaters of the current that flows out of the Bering Sea and into the Chukchi Sea. Breeding seabirds throughout the northern Bering Sea–eastern Chukchi Sea region may be related, therefore, by common food web dependencies that are influenced by similar physical processes.

If energy flow through food webs in northern Alaskan waters waxes and wanes in response to patterns of environmental change during intervals of a few years, as it apparently did in the 1970's, it might also adjust to longer term fluctuations in the environment (see Cushing and Dickson 1976; Walsh 1978). For example, between the late 1940's and mid-1960's, sea-surface temperature over the bulk of the northern Pacific Ocean (15–60°N and 130°E–110°W) was generally normal or above; only three years in the mid-1950's were slightly below normal (Namias and Cayan 1981). Since 1964, however, sea-surface temperature has been above normal in only three years. Such differences in the physical environment might alter energy budgets in northern Alaska sufficiently to account for the large declines in numbers of murres that we have documented at Bluff and at Cape Thompson (Springer et al. 1984). Below-average temperatures for many years could have resulted in relatively less energy available to murres, relatively low levels of natality, and the recent numerical decline as recruitment fell below adult mortality. At Cape Thompson, murre numbers were highest in 1960, a time when water temperatures had been above normal for several preceeding years. However, relatively cold temperatures prevailed from the mid-1960's until 1976. A simulation analysis predicted that murre numbers at Bluff would increase beginning in 1983 (Springer et al. 1984), a consequence of improved reproductive success associated with the recent warming trend, if the population decline resulted from climatic fluctuations and not other causes.

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Effects of Fluctuations in Hydrographic Conditions on Year-Class Strength of American Shad (*Alosa sapidissima*) in the Connecticut River

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We evaluated a parent–progeny relationship for Connecticut River shad, *Alosa sapidissima*, with population data from 1966 through 1982. The hypothesis that shad year-class strength is established during larval development mainly by abiotic factors was assessed by correlation analysis between environmental variables, year-class strength, weekly zooplankton densities, hydrographic conditions, and larval feeding success among the 1979 through 1982 year-classes. No significant parent–progeny relationship was found for American shad even after recruitment variations due to river flow and water temperatures were removed. All three environmental variables (mean river discharge, water temperatures, and total monthly precipitation) were significantly correlated with shad year-class strength for the month of June, the period when most American shad larvae emerge.

On évalue la relation parent–progéniture chez l'alose savoureuse (*Alosa sapidissima*) du Connecticut à l'aide de données sur la population recueillies de 1966 à 1982. Grâce à une analyse de corrélation entre les variables environnementales, l'abondance des classes d'âge, les densités hebdomadaires de zooplancton, les conditions hydrographiques et le succès des larves à l'alimentation chez les classes d'âge de 1979 à 1982, on étudie l'hypothèse selon laquelle l'abondance d'une classe d'âge serait déterminée principalement par les facteurs abiotiques pendant le développement larvaire. Aucune relation parent–progéniture significative n'a été découverte chez l'alose savoureuse, même l'élimination des variations du recrutement causées par le débit et la température de l'eau. Les trois variables environnementales (débit moyen, température de l'eau et précipitation mensuelle totale) étaient en corrélation nette avec l'abondance des classes d'âge en juin, le mois où la plupart des larves d'alose savoureuse émergent.

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Year-class strength of Connecticut River shad, *Alosa sapidissima*, appears to be established by the end of the larval period (Crecco et al. 1982, 1983). However, it is less certain whether larval survival rates and ultimately year-class recruitment are mainly influenced by biotic factors (food availability and predation), abiotic factors (river temperature and flows), or their joint interaction with egg production. Various hypotheses have been offered to explain how biotic and abiotic factors interact to influence recruitment levels among many fish stocks (Hjort 1926; Hempel 1965; May 1974; Cushing 1971; Frank and Leggett 1982). One of the most well-known and provocative is the "match–mismatch" hypothesis (Cushing and Dickson 1976) in which temporal and spatial changes in climatic and hydrographic events affect the timing of critical life cycle events, such as between larval fish emergence and food availability, as well as between egg and larval production and the presence of key predators.

There are a number of studies of American shad (Marcy 1976; Leggett 1977) and other fishes (Walford 1938; Carruthers 1951; Christie and Regier 1973; Sissenwine 1977) that have statistically linked climatic and hydrographic variations to year-class success, but these studies have seldom provided insight about the causal mechanisms by which climatic factors influence year-class strength. The dangers of using retrospective correlation analysis to infer causality without a firm understanding of direct or indirect mechanism(s) have been discussed (Gulland 1965; Bakun and Parrish 1980).

A more useful approach to climate–fisheries studies, as recommended by Austin and Ingham (1978), is to offer a working hypothesis, and then test its validity with empirical data and a thorough statistical analysis. In this paper, we followed their approach and tested the hypothesis that year-class strength of Connecticut River shad depends mainly on climatic and hydrographic conditions during larval development. We examined temporal fluctuations in hydrographic conditions in the Connecticut River with changes in the distribution and abundance of American shad larvae, their feeding success, and their food supply between strong and weak year-classes. A parent–progeny relationship for American shad was also assessed, as well as the statistical relationships between American shad year-class strength and total monthly precipitation, mean monthly river discharge, and water temperatures from 1966 through 1973 and from 1978 through 1982.

Methods

A correlation analysis was conducted between the relative strength of the 1966–73 and 1978–82 year-classes and mean

monthly river flows, water temperatures, and total monthly precipitation data. Support for the hypothesis that year-class strength is determined by hydrographic and meterological factors during the early stages of larval development would be demonstrated if all three environmental factors were significantly correlated to year-class strength only during the month of June, the period of primary larval development in the Connecticut River (Cave 1978; Crecco et al. 1983). On the other hand, if significant correlations take place for environmental data during June, as well as during the months of shad egg development (April–May), juvenile development (July–October), and/or during the remaining months, the analysis would not support the hypothesis.

The index of year-class strength was defined as the mean catch-per-effort (CPE) of juvenile American shad taken in weekly collections from mid-July through mid-September (Marcy 1976; Crecco et al. 1981). No juvenile shad sampling was conducted from 1974 through 1977, thus accounting for the gap in the data base. We assumed that the relative strength of the 1966–73 and 1978–82 year-classes was determined accurately by juvenile CPE data. Evidence in support of this assumption was reported by Crecco et al. (1983) in which a significant positive relationship ($r = 0.92$, $P < 0.001$) was found between the mean juvenile CPE index for the 1966–73 year-classes and the corresponding number of virgin female shad from these year-classes in the adult spawning runs. Male population data were not used to calculate adult recruitment levels, as their age structure and commercial catch data are biased by gill net selectivity and underreporting (Leggett 1976; Crecco et al. 1982).

River flow, water temperature, and precipitation data were chosen as environmental variables for two reasons. Studies of other fishes have also shown that hydrographic and climatic factors affect the phase and amplitude of zooplankton production (Cushing 1973; Jones and Hall 1974), the rate at which fish eggs and larvae develop (Steele and Edwards 1970), transport of larvae to suitable nursery areas (Nelson et al. 1977; Parrish and MacCall 1978), and physical injury to the eggs and larvae (Pinus 1974; May 1974). Also, long-term data were available for daily river flows, water temperatures, and monthly precipitation levels. These were recorded close to the major shad spawning areas in the Connecticut River. River flow rates (cubic metres per second) were taken at Thompsonville, Connecticut (river km 89), by the U.S. Geological Survey (1928–82) whereas water temperatures were taken at the Holyoke Dam (river km 120) by the Holyoke Water Power Company (unpubl. reports). Total monthly precipitation (millimetres from 1966 to 1982 were taken by the National Weather Service at Bradley Field Airport in Windsor Locks, Connecticut.

Juvenile American shad (> 35 mm TL) were collected weekly at seven stations between Holyoke, Massachusetts (river km 107), and Essex, Connecticut (river km 5), from mid-July through mid-October 1978–82. The juvenile sampling gear and seine sites are similar to those of the 1966–73 studies (Marcy 1976). This was to make the 1978–82 juvenile CPE values as comparable as possible with the 1966–73 data. Further details on juvenile sampling methods are given in Crecco et al. (1983).

The mean annual juvenile index (Y) was fitted to mean monthly river flow, water temperature, and total monthly precipitation values (X) with exponential

$$Y = ae^{bX}$$

and power

$$Y = aX^b$$

curves using log transformed variables. The use of these models was justified, given that environmental factors usually exert a multiplicative influence on fish production (Ricker 1975).

As a further test of our hypothesis we evaluated the extent to which the relative abundance of American shad larvae and their feeding incidence vary temporally with changes in zooplankton density (number per cubic metre), precipitation, river flows, and water temperatures from 1979 to 1982. This analysis was designed to determine differences in zooplankton densities and environmental conditions between strong and weak year-classes.

Shad larvae were collected weekly at 8–12 sites in the Connecticut River with a 6.1-m plankton bag seine (2.4 m deep, wing and bag mesh of 0.5 mm) and 30-m lead ropes from May 15 to July 15, 1979–82. All seine sites were located north of the Enfield Dam (river km 87–180), well within the major spawning areas for American shad (Layzer 1974; Cave 1978). The composition and abundance of river zooplankton were determined weekly from two or three replicate samples collected at four of the larval seine sites using a Clark–Bumpus plankton sampler fitted with an 80-μm mesh net. Only cladocerans, copepods, and immature insects were counted and identified to genus. Further details on sampling methods and analytical procedures used to estimate zooplankton and larval shad abundance are given in Crecco and Blake (1938).

The percentage of American shad larvae with zooplankton in their stomachs, defined as the feeding incidence, was determined for 30–60 shad larvae (10–13 mm TL) from each weekly collection from mid-May through mid-July 1979–82. Larger larvae were not analyzed, as they usually were full of food. American shad larvae used for food analysis were chosen randomly from all sites within a weekly collection. Larval stomachs were examined under a compound microscope (10×) and all ingested organisms were identified to genus. The mean feeding incidence for each year was estimated by weighting each of the weekly feeding incidence rates by the number of shad larvae taken in that week. This weighting procedure was used to better quantify the overall match or mismatch between larval feeding success and larval abundance among the four year-classes. The relationships between the arc sine of the weekly feeding incidence rates and weekly mean zooplankton densities, river flows, and temperatures were examined with linear and curvilinear regressions. The logs of the mean weekly zooplankton densities and weekly river flows were used to insure that the assumptions of parametric regressions were fulfilled (Draper and Smith 1981).

To examine the existence of a parent–progeny relationship for American shad we used adult recruitment and spawning stock data from 1966 to 1982. Adult recruitment was defined as the sum of virgin female shad of year-class t in the female spawning runs during years $t + 4$, $t + 5$, and $t + 6$. Year-class strength was not computed beyond the 1977 year-class, as the more recent year-classes have not yet been fully recruited to the spawning populations. The spawning stock is defined as the female shad population for each year minus the sport and commercial catches. This procedure was necessary because the main spawning areas (river km 80–190) are located upriver of the commercial and most of the sport fishing areas. The Ricker, Beverton–Holt, and Cushing spawner–recruit models (Cushing 1971; Ricker 1975) were fitted to the data with log transformed

variables. These models were also fitted by a nonlinear least squares procedure (Ralston and Jenrich 1978).

It has been suggested that environmental effects on recruitment may mask a potential density-dependent relationship between parents and progeny (Nelson et al. 1977). Therefore, stage regression analysis (Draper and Smith 1981) was also used to adjust the recruitment values to average conditions of water temperature and river flow. The procedure was to add the residuals from the relationship between recruitment and environmental variables to the mean logarithmic value of recruitment. The adjusted recruitment values were transformed to the arithmetic scale and plotted against the levels of escapement from 1966 to 1977.

Results

Stock–Recruitment Relationship

There was no significant stock–recruitment relationship using female shad population data from 1966 through 1977 (Fig. 1). Neither linear nor nonlinear spawner–recruit models could account for more than 6.5% of the recruitment variation (Table 1). The very strong 1971 year-class and the very weak 1973 cohort were both produced by relatively small parent stocks, indicating that year-class strength of Connecticut River shad is independent of egg production over the range of escapement observed during 1966–77. When the variation due to June river discharge and water temperature on shad year-class strength was removed, the Ricker parent–progeny model accounted for 11% of the remaining variation (Table 1), although this was not significant. Because strong and weak year-classes of American shad arise from a wide range of excapement levels, we suggest that year-class strength of Connecticut River American shad is primarily determined by differential mortality during the prerecruit phase.

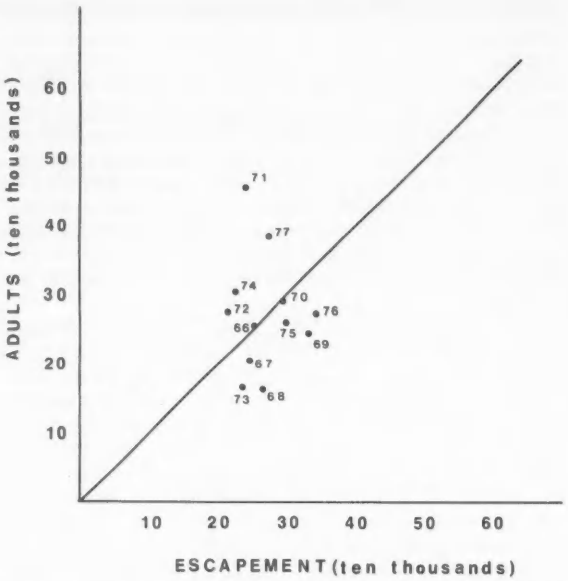

FIG. 1. Stock–recruitment relationship for Connecticut River American shad with 45° transfer line (numbers are year-classes).

TABLE 1. Linear and nonlinear stock–recruitment models for Connecticut River shad.

Model	Equation	R^2
Linear Equations		
Ricker	$R = 2.621e^{-0.00362P}$	0.02
Cushing	$R = 276.552P^{-0.0087}$	0.02
Beverton–Holt	$R = 1/(0.0033 + 0.1655P)$	0.07
Nonlinear Equations		
Ricker	$R = 3.114e^{-0.00411P}$	0.03
Cushing	$R = 585.580P^{-0.1358}$	0.02
Beverton–Holt	$R = 1/(0.0030 + 0.1753P)$	0.08
Linear Adjusted for Environmental Factors		
Ricker	$R = 4.174Pe^{-0.00535P}$	0.11
Cushing	$R = 176.44P^{-0.0087}$	0.01
Beverton–Holt	$R = 1/(0.0053 + 0.3654P)$	0.08

Hydrographic Fluctuations and Shad Year-Class Strength

Correlations between juvenile CPE values and monthly mean river flows, water temperatures, and total monthly precipitation were significant only for the month of June (Fig. 2, 3, 4), when most larval American shad emerge. Correlation coefficients for all other months were generally less than 0.30 (Table 2). Both exponential and power regressions showed that shad year-class strength was inversely related to mean June river flows and total June precipitation but was positively correlated with mean June river temperatures. Total precipitation and mean flow during June 1971 were among the lowest ever recorded (U.S. Geological Survey 1928–82) and the resultant year-class is the strongest in 17 yr. Similarly, the mean river flow in June 1980 was similar in magnitude to the 1971 levels and the 1980 year-class was the second strongest. By contrast, the failure of the 1968, 1972, and 1982 year-classes was associated with low water temperatures and record high levels of total June rainfall and river flows.

There was a significant colinearity among the three environmental variables. Mean June temperature was inversely related to mean June river flow ($r = -0.893, P < 0.001$) and total June precipitation ($r = -0.882, P < 0.001$) whereas June river flow was positively correlated ($r = 0.793, P < 0.025$) with total June precipitation. This interrelationship among environmental variables was anticipated, as rainfall levels during late May and June are expected to enhance the volume of June river flow and reduce the water temperature.

Larval Feeding Incidence

Gut content analysis of 1260 American shad larvae captured between 1979 and 1982 showed that weekly feeding incidence values were consistently low (0–6.9%) from May 20 through June 1 and increased abruptly (20–60%) after mid-June (Table 3). The feeding index varied among the years but was highest and most persistent for the strong 1980 year-class, intermediate for the moderately weak 1979 and 1981 year-classes, and lowest for the very weak 1982 cohort. When the weekly feeding incidence data were adjusted for changes in larval abundance, the adjusted mean feeding incidence was twice as high in 1980 than in 1982 and 1981 and 46% higher than in 1979 (Table 4).

There was a relationship between larval feeding success, hydrographic events, and year-class strength from 1979 through 1982 (Table 4). The intense rainfall and record high river flows in June 1982 were associated with record low June water

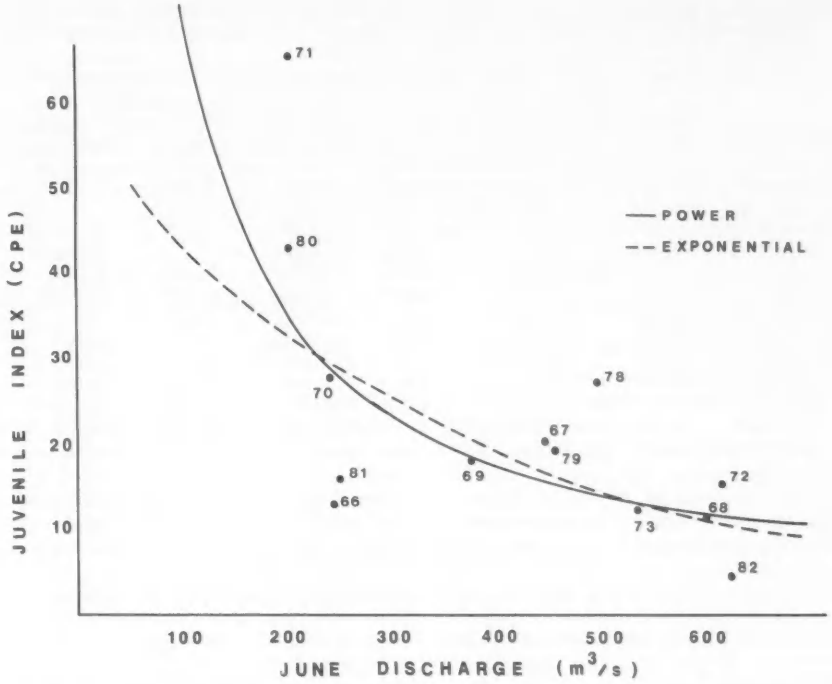

FIG. 2. Juvenile index from 1966–73 and 1978–82 versus mean June river discharge fitted to both power and exponential curves (numbers are year-classes).

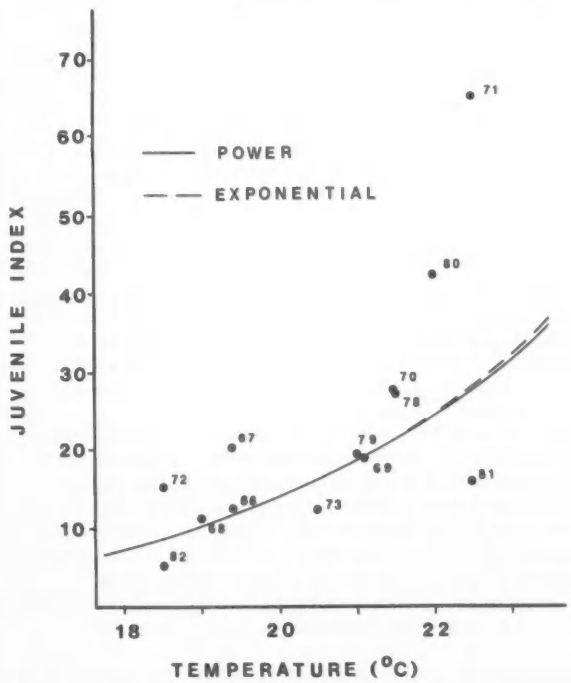

FIG. 3. Juvenile index from 1966–73 and 1978–82 versus mean June river temperatures fitted to both power and exponential curves (numbers are year-classes).

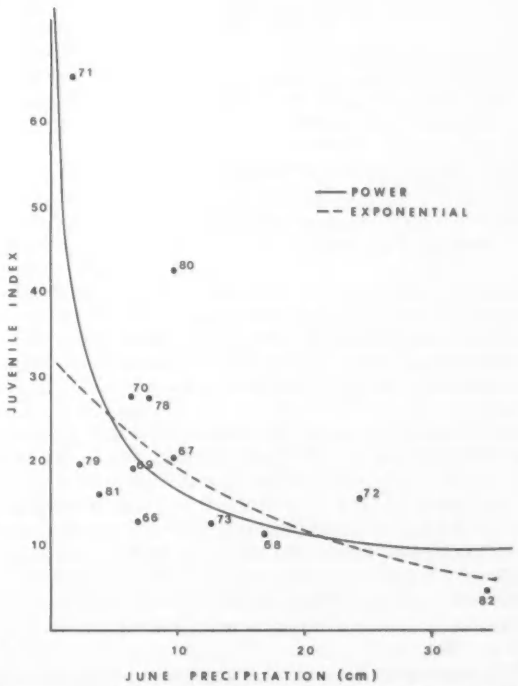

FIG. 4. Juvenile index from 1966–73 and 1978–82 versus total June precipitation fitted to both power and exponential curves (numbers are year-classes).

TABLE 2. Correlation coefficients of mean monthly river flow, water temperature, and monthly rainfall to shad year-class strength in the Connecticut River (+, correlation values 0.01; *significant correlation at $P < 0.05$; **significant correlation at $P < 0.01$).

	Temperature		River flow		Rainfall	
Model	Power	Exponential	Power	Exponential	Power	Exponential
January	−0.148	−0.184	−0.200	−0.190	−0.209	−0.078
February	−0.257	−0.233	−0.260	−0.250	−0.063	+
March	−0.305	−0.321	−0.170	−0.250	0.205	−0.272
April	−0.173	−0.296	0.050	0.030	+	−0.045
May	−0.158	−0.130	0.360	0.270	−0.148	−0.110
June	0.634*	0.632*	−0.680*	−0.630*	−0.673*	−0.710**
July	0.365	0.363	−0.490	−0.420	0.045	0.032
August	−0.032	−0.032	−0.070	−0.130	+	0.063
September	−0.071	−0.084	0.050	−0.040	−0.071	−0.045
October	−0.071	−0.055	0.230	0.060	−0.077	−0.045
November	+	0.063	0.180	0.120	0.184	0.155
December	−0.210	−0.152	+	0.080	−0.071	−0.105

TABLE 3. Relationship between the weekly larval feeding incidence, the number of shad larvae (10–13 mm) captured, and weekly zooplankton densities among the 1979–82 year-classes in the Connecticut River

	Collection Dates								
	May 20–23	May 28–30	June 1–3	June 8–11	June 15–17	June 22–24	July 1–3	July 8–10	July 15–18
1979									
Feeding incidence (%)	0.0	6.8	12.0	22.5	22.0	33.3	50.0	55.0	—
Number of larvae examined	45	43	25	40	41	46	38	40	—
Number of larvae captured	5992	3200	405	2 218	10 648	14 791	3021	2656	—
Zooplankton density (N/m^3)	496	558	532	548	722	1 808	1899	2247	—
1980									
Feeding incidence (%)	0.0	6.9	32.0	37.5	30.4	56.0	64.0	60.0	55.0
Number of larvae examined	39	29	25	24	23	25	25	25	20
Number of larvae captured	397	4391	11 284	8 701	9 345	5 765	5786	862	102
Zooplankton density (N/m^3)	222	1319	2 822	2 527	2 838	4 187	1448	939	735
1981									
Feeding incidence (%)	0.0	0.0	9.4	8.5	41.4	39.0	20.5	26.1	—
Number of larvae examined	10	35	64	59	58	49	23	23	—
Number of larvae captured	64	1942	15 631	36 878	9 941	8 154	3181	1022	—
Zooplankton density (N/m^3)	707	1040	1 357	1 308	398	349	157	246	—
1982									
Feeding incidence (%)	0.0	2.3	6.3	10.7	26.8	12.2	28.6	22.5	60.6
Number of larvae examined	24	42	32	28	41	57	28	40	33
Number of larvae captured	66	5566	17 761	15 546	13 337	7 656	5220	2783	921
Zooplankton density (N/m^3)	424	866	803	732	755	520	734	217	172

temperatures. These conditions corresponded with the lowest and least persistent zooplankton densities, the lowest larval feeding incidence, and the smallest year-class in 17 yr. These hydrographic and biotic conditions were completely reversed for the strong 1980 year-class. June river temperatures, river flows, zooplankton densities, and larval feeding incidence in 1979 were intermediate in magnitude between those in 1980 and 1982. The low larval feeding incidence in 1981 was associated with weekly June zooplankton densities that were much lower than in 1980.

The relationship between the arc sine of the weekly feeding incidence and mean weekly river temperatures from mid-May through mid-June was always positive and significant from 1979 through 1982 (Table 5). The correlations between the arc sine of the feeding incidence and the log of the mean weekly river flows from May through June were negative and statistically significant for all years except 1982. The strength and direction of the correlations between larval feeding success and the log of the mean weekly zooplankton densities were inconsistent among the four years (Table 5). There was a significant positive correlation between weekly larval feeding incidence and zooplankton density in 1979; it was strongly negative in 1981 and 1982 and weakly positive in 1980.

Discussion

Several hypotheses can be offered to explain the lack of a stock–recruitment relationship for Connecticut River American

TABLE 4. Relationship of larval shad feeding success to year-class strength, mean zooplankton density, and mean June river flow, 1979–82, in the Connecticut River.

Year	Juvenile index	Larval feeding incidence (%)	Adjust feeding incidence (%)	Zooplankton density[a]	June flow[b]
1979	19.6	25.2	25.8	1010	448
1980	42.7	34.9	37.6	1714	202
1981	16.0	16.1	16.7	620	313
1982	4.7	19.4	14.6	580	622

[a]Mean zooplankton density (N/m^3) collected weekly from May 15 through June 15, 1979–82.

[b]June flow represents the mean flow for the month in m^3/s.

shad. First, shad year-class strength might be regulated by environmental factors over the normal range of escapements, but density-dependent regulations could become important when parent stock falls below or exceeds some boundary levels (Beverton 1962). An alternative hypothesis is that shad recruitment depends on environmental fluctuations to the extent that the true underlying stock–recruitment relationship is totally obscured (Nelson et al. 1977). This second hypothesis is doubtful for American shad, as there was no significant parent–progeny relationship after the residual variation due to environmental factors was removed (Table 1). The first hypothesis is consistent also with the high fecundity (Leggett 1969) and high incidence of repeat spawning (Leggett and Carscadden 1978) of Connecticut River shad, which may be an evolutionary adaptation to stabilize the population in the presence of environmental uncertainty.

Ricker (1954) and Cushing (1981) recognized that a statistically significant parent–progeny relationship requires a large data base and a wide range of escapement values. We recognize that our conclusions for American shad may be premature given only 12 yr of data and a narrow range of escapements. Nonetheless, the poor fits observed for the three parent–progeny models (Table 1) indicate that more than a century of additional stock–recruitment data are required to make the relationship significant. Current management needs make this unacceptable. While our findings conflict with those of earlier shad studies (Walburg 1963; Leggett 1976), most stock–recruitment studies conducted on other herring have shown that recruitment fluctuations were independent of parent stock size (Burd and Holford 1971; Dragesund and Nakken 1973; Gulland 1973: Bowers and Brand 1973; MacCall 1979). Only salmonid studies (Larkin and Hourston 1964; Chadwick 1982) have demonstrated consistently that parent–progeny models provide a useful predictive capability.

In the absence of a statistically significant stock–recruitment relationship, it is generally assumed that year-class strength of most herring fishes is established by differential mortality during or shortly after the larval drift (Gulland 1965; May 1974; Cushing and Dickson 1976). Support for the hypothesis that year-class strength of American shad is determined by hydrographic conditions in June was given by significant correlations between June environmental factors and shad year-class strength and the lack of significant correlations among all other months (Table 2). We conclude that high larval mortality and year-class failure is linked to high rainfall and high river flows during June. These findings are in accord with an earlier study on the Connecticut River (Marcy 1976) in which June river flows and water temperatures were significantly correlated with shad year-class strength from 1966 through 1973. Leggett (1977) also demonstrated that June temperatures and June river flows were related to deviations from the stock–recruitment relationship of American shad.

The correlation analysis supports our hypothesis that temporal fluctuations in June rainfall, river flows, and water temperatures directly or indirectly affect larval mortality and year-class strength of American shad. Whereas causal relationships derived from correlation analysis alone may be misleading (Gulland 1965; Bakun and Parrish 1980), our hypothesis was further corroborated by the differences in zooplankton densities, river hydrography, and larval feeding success between strong and weak year-classes. These data suggest that high June river flows and low river temperatures reduce larval feeding success, survival, and ultimately shad year-class strength, providing a reasonable explanation for the lack of a parent–progeny relationship.

Differential egg mortality could also account for large fluctuations in year-class strength (Marr 1956; May 1974). This hypothesis could not be evaluated directly for American shad because egg mortality data are unavailable between strong and weak year-classes. However, the correlations between environmental factors and year-class strength were always low during May, the main period of shad egg development (Marcy 1976; Layzer 1974). Therefore, it is unlikely that differential egg mortality alone could account for the observed year-class fluctuations of American shad.

The hypothesis that food availability and environmental conditions cause differential larval mortality and year-class fluctuations was first advanced by Hjort (1926). His "critical period" hypothesis has been assessed by Lasker (1975, 1978) who reported that year-class strength of northern anchovy, *Engraulis mordax*, was established associated with the timing and intensity of upwellings during larval development. Likewise, Walsh et al. (1980) noted that ocean storms and frequent upwellings influence the distribution of plankton and larval survival of Peruvian anchovy, *Engraulis ringens*. Evidence from other ocean studies demonstrated that upwelling events affect larval mortality and year-class strength (Bakun 1973; Bakun and Nelson 1977; Parrish and MacCall 1978; Parrish et al. 1981), and it is usually assumed that food limitation is the primary cause.

The relationship between water currents and cohort strength has not been studied extensively for freshwater and estuarine species. Turner and Chadwick (1972) reported a significant positive correlation between river flows in the Sacramento–San Joaquin Estuary and year-class strength of striped bass, *Morone saxatilis*. Hayman and Tyler (1980) found an inverse correlation between Columbia River flows and year-class strength of Dover sole, *Microstomus pacificus*, as did Bulkley and Benson (1962) for cutthroat trout, *Salmo clarki*, in Utah streams.

The mechanisms by which hydrographic turbulence brings about changes in larval shad survival are uncertain because daily river flow and rainfall levels are nonlinear, time-dependent processes (Sharp 1980) that may act singularly or in combination with other factors. The potential interactions of flow rates with climatic, physical, and biological processes are numerous (Turner and Chadwick 1972) and include depression of the water temperatures, which retards the onset and duration of shad spawning (Leggett and Whitney 1972), the growth rates of larvae (Murai et al. 1979), and the production of riverine zooplankton (Chandler 1937; Beach 1960). High river flows

TABLE 5. Linear regressions between the arc sine of the weekly larval feeding incidence (Y) and mean weekly water temperatures, log mean river flows, and mean weekly zooplankton densities (N/m^3) from 1979 through 1982 in the Connecticut River (*significant at $P < 0.05$ level or higher).

Year	Feeding incidence vs. water temperature	Feeding incidence vs. river flow	Feeding incidence vs. zooplankton density
1979	$Y = -48.14 + 3.19X$ $r = 0.854$ $F = 16.18$*	$Y = 81.40 - 11.14X$ $r = -0.786$ $F = 9.67$*	$Y = -99.80 + 16.90X$ $r = 0.925$ $F = 35.94$*
1980	$Y = -69.48 + 4.34X$ $r = 0.946$ $F = 59.04$*	$Y = 192.14 - 31.22X$ $r = -0.887$ $F = 25.82$*	$Y = -17.90 + 5.63X$ $r = 0.354$ $F = 1.00$
1981	$Y = -64.63 + 3.87X$ $r = 0.769$ $F = 8.70$*	$Y = 179.06 - 27.55X$ $r = -0.659$ $F = 4.60$*	$Y = 99.20 - 12.90X$ $r = -0.636$ $F = 4.07$*
1982	$Y = -56.30 + 3.54X$ $r = 0.768$ $F = 8.70$*	$Y = 95.84 - 13.71X$ $r = -0.466$ $F = 1.94$	$Y = 87.20 - 12.20X$ $r = -0.633$ $F = 4.68$*

may reduce the transparency of the water and the ability of fish larvae to see their prey (Theilacker and Dorsey 1980). Low transparency resulting from high flows can also interfere with photosynthesis and river phytoplankton production, causing the selective elimination of major larval prey such as filter-feeding cladocerans and copepods (Chandler 1937; Hynes 1970). Finally, high river flows may dissipate the microscale patchiness of river zooplankton, leading to unfavorable feeding conditions for first-feeding larvae (Lasker 1975; Smith 1978). Given the myriad of pathways through which river flows could affect zooplankton availability and larval shad survival, it is unreasonable to expect that a single causal mechanism can operate under all circumstances.

The significant correlations between weekly environmental variables and larval feeding incidence show that hydrographic fluctuations influence the degree to which shad larvae can capture food. However, the determination of causal mechanisms is confounded by colinearity among the environmental variables. For example, June water temperatures and transparency increase when June river flows decline, so it is uncertain whether the significant inverse correlations between weekly flows and larval feeding success (Table 5) are directly related to flows, or to an increase in larval metabolism resulting from rising temperatures, and/or to improved feeding conditions brought about by higher visibility.

The inconsistent correlation between weekly zooplankton densities and larval feeding success from 1979 through 1982 (Table 5) is difficult to explain. One interpretation is that zooplankton density is less critical to larval feeding success than the prolonged periods of low and stable river flows, which cause a steady rise in water temperatures and transparency. Another possibility is that the periodicity and duration of peak zooplankton production may be more instrumental to larval survival than actual zooplankton density. Lasker and Smith (1977) concluded that survival rates of northern anchovy larvae depended mainly on the synchrony between production cycles of larvae and their food supply. Also, the strong negative correlations between zooplankton densities and larval feeding success in 1981 and 1982 may have been due to selective grazing by larger shad larvae and their cogeneric, the blueback herring, *Alosa aestivalis* (Wells 1970; Burbridge 1974).

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NOTES

Sites of Uptake of Geosmin, a Cause of Earthy-Flavor, in Rainbow Trout (*Salmo gairdneri*)

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To identify absorption sites of earthy-flavor in rainbow trout (*Salmo gairdneri*), we placed the geosmin-producing algae *Symploca muscorum* on four locations. We showed that the most rapid absorption occurred in the gills (6 min), followed by the skin (1.5 h), small intestine (4 h), and stomach (7 h). In trout farming, if ingestion of algae is reduced, then the most significant route of uptake of geosmin will be through the gills and skin.

Dans le but d'identifier les sites d'absorption du goût de terre chez la truite arc-en-ciel (*Salmo gairdneri*), les auteurs ont placé l'algue productrice de géosmine, *Symploca muscorum*, à quatre différents endroits sur le corps du poisson. Ils montrent que l'absorption la plus rapide a lieu à la hauteur des ouïes (6 min), puis de la peau (1,5 h), du petit intestin (4 h) et de l'estomac (7 h). Si l'ingestion d'algues est réduite dans les trutticultures, la principale voie d'absorption de la géosmine sera donc par les ouïes et la peau.

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Certain Cyanophyceae, or blue-green algae (Leger 1910; Lovell and Sackey 1973), and actinomycetes (Thaysen 1936; Thaysen and Pentelow 1936) are well-known sources of earthy-flavor in fish. An earthy-flavor producing compound, geosmin, was isolated and characterized from actinomycetes (Gerber and Lechevalier 1965). Safferman et al. (1967) showed that it was also geosmin that gave some Cyanophyceae their characteristic smell. Geosmin is the principal compound responsible for the earthy-flavor in fish (Yurkowski and Tabachek 1974).

The sites of uptake of earthy-flavor in fish have been discussed but not thoroughly studied. Thaysen (1936) and Thaysen and Pentelow (1936) concluded that the Atlantic salmon (*Salmo salar*) absorbs the taint principally through the gills into the blood stream; the blood carries it to the muscles. They showed no evidence for absorption through the skin but suggested that absorption might occur in the stomach from ingested water. Lovell and Sackey (1973) showed that when channel catfish (*Ictalurus punctatus*) are placed in tanks containing cultures of geosmin-producing cyanophytes, the taint in fish develops in less than 24 h, but when the fish are receiving filtered water from cultures of cyanophytes, the taint develops more slowly (10 d before the taint is as strong as after 24 h in the unfiltered culture). They concluded that ingestion of algae aids in taint acquisition. Persson (1980) suggested that the uptake of earthy-flavor in fish increases during feeding, but usually it is sufficient for the earthy-odor compounds to be present in the water to taint the fish. In the latter case, Persson noted that the major route of uptake is probably across the gill membrane.

In our opinion the sites of absorption of earthy-odor compounds have not been unequivocally found. Placed in algae-free water, the fish can acquire the earthy-flavor through ingested water as well as through the gills. The skin can also be a site of absorption. A faster absorption of earthy-flavor by fish placed in algae-containing water could be due to higher concentration of earthy-flavor compounds and not necessarily caused by ingestion of the algae.

The purpose of our study was to identify the major sites of uptake of geosmin in rainbow trout (*Salmo gairdneri*) and to try to explain the significance of these sites with respect to trout culture.

Materials and Methods

The cyanophyte *Symploca muscorum* (1478–1), which we used as a geosmin source, was obtained from the Culture Center of Algae and Protozoa in Cambridge, U.K. The algae were cultured aseptically according to Safferman et al. (1967). We did not identify the earthy-flavor compound produced by these algae, but according to the literature (Safferman et al. 1967; Medsker et al. 1968; Tabachek and Yurkowski 1976) the compound is geosmin.

Rainbow trout from the Danish Trout Culture Research Station, weighing approximately 300 g, were anaesthetized with 0.5 mL of tubocurarine chloride (0.3 mg/mL) intrave-

nously and placed on their side on a foam rubber pad, which was out of water. By a plastic tube placed in the mouth, the fish were supplied with tap water (200 mL/min) saturated with air at an ambient temperature of 15°C. The head protruded from the foam rubber pad, so the water could run freely, and only the gills on the underside were irrigated with water. The pulse rate (50–100/min) and respiration rate (1–100/min) were monitored. The respiration rate was used to evaluate the depth of the anaesthesia. The oxygenation of the gills was independent of respiration rate, as gills were irrigated by means of a waterflow. On signs of body movement that occurred approximately every 2 h, the fish was given 0.1 mL of tubocurarine chloride (0.3 mg/mL) intramuscularly. If necessary, the anaesthesia was adjusted by giving 0.05 mL of neostigmine bromide (0.05 mg/mL) and 0.05 mL of atropine (10 mg/mL) intramuscularly.

Four experiments were designed to show absorption of geosmin, if any, by four isolated sites in rainbow trout. The algae, *Symploca muscorum*, were sedimented by centrifugation of 80 mL of suspended culture for 10 s at 180 × *g*. The dry weight of the residue was 0.02 g/mL, which was determined by drying at 45°C for 4 d. The residue was sucked up in a syringe (luer conus aperture 2 mm) and placed on a chosen site of different fish for different time periods until the absorption time for the earthy-flavor was determined. First, increasing exposure times were used to get an idea of the hours involved. When strong earthy-flavor was obtained, the fish were tasted at smaller intervals to determine the absorption times more precisely. After each trial the fish was tasted to ascertain the intensity of earthy-flavor obtained after a given time of exposure. Because the algae were obtained from the same culture, we assumed that each millilitre of algae contained the same concentration of geosmin. In each experiment we used 1 mL of algae at each site. Four experiments were performed.

(1) The algae were placed only on the gills at the fish's top side. Algal contact with the skin was prevented by placing parafilm on both sides of these gills. An inflated balloon catheter in the oesophagus prevented the fish from swallowing the algae. Fish were sampled and tasted in the following sequence: 1, 2, 3, 2.5, 1.5, 0.5, 0.25, 0.1, and 0.05 h.

(2) The algae were evenly dispersed on the whole skin surface of the fish caudally from the end of the pectoral fin rays at the top side. Fish were sampled and tasted in the following sequence: 2, 4, 6, 5, 3, 1, and 1.5 h.

(3) The algae were injected via the rectum into the small intestine by means of a cholodocus cannulla. Fish were sampled and tasted in the following sequence: 2, 4, and 3 h. We continued these experiments with algae placed in the small intestine only until slight earthy-flavor was obtained because algae are not naturally exclusively present in the small intestine. The experiments were to determine if geosmin could be absorbed by parts of the gastrointestinal tract other than the stomach.

(4) A balloon catheter was placed and inflated in the oesophagus. The hollow tube of the catheter, which ended in the stomach, was then connected to the syringe containing algae and the algae placed in the stomach. As the oesophagus was blocked with the inflated balloon, the fish were prevented from regurgitating the algae onto the gills. Fish were sampled and tasted in the following sequence: 6, 8, 10, 12, 14, 13, 10.5, and 7 h.

In all experiments the application of algae was omitted for the controls.

After the absorption period the fish were killed, cleaned, and filleted. The fillets were separately wrapped tightly in aluminium foil and cooked for 10 min immersed in water. Only fillets were cooked because the skin in experiment 2 probably would have an earthy-flavor that could interfere with the flavor of the flesh. In experiment 2 the two fillets were cooked in different pots to determine a possible difference in taste, as only the one side of the fish had been in contact with the algae. The fillets were categorized as having no, slight, medium, or strong earthy-flavor by five taste panelists from the Trout Culture Research Station. The fillets were tasted hot and at room temperature.

TABLE 1. Minimum time required to obtain earthy-flavor in rainbow trout after exposure to geosmin.

	Earthy-flavor (h)		
	Slight	Medium	Strong
Gills	0.1	1.0	2.5
Skin	1.5	3.0	6.0
Small intestine	4.0		
Stomach	7.0	10.5	14.0

Results

The earthy-flavor in rainbow trout was acquired most rapidly via the gills, followed in descending order by the skin, small intestine, and stomach (Table 1). There was no difference in the earthy-flavor intensity of the two fillets from the same fish. The earthy-flavor, if present, tended to be more pronounced when the fish were tasted cold. This difference was so small that the categorization did not depend on the temperature of the tasted fish. Earthy-flavor was not detected in control fish.

Discussion

Under our experimental conditions an earthy-flavor was acquired by rainbow trout most rapidly through the gills followed by slower rates through the skin, small intestine, and stomach. Under natural conditions, water or algae ingested by the fish must go through the stomach before reaching the small intestine. Acidity in the stomach, if present, can transform geosmin to an odorless compound, argosmin (Gerber and Lechevalier 1965), during absorption in the stomach and transit to the small intestine. This transformation is obviously not instantaneous and geosmin will be present in the stomach, but the concentration will be smaller, if acidity is present, than the concentration when the algae is placed in the small intestine via the rectum. Possibly, the major uptake of geosmin in the gastrointestinal tract is in the small intestine. If so, the different intensities of earthy-flavor we obtained when algae were placed in the stomach could be caused by uptake via the small intestine after the algae passed through the stomach. This view is supported because it took 3 h before the algae could be detected in the small intestine. This is equal to the difference between the time it took to obtain slight earthy-flavor when algae were placed in the stomach and in the small intestine. The absorption time in the stomach alone can only be revealed by clamping the connection between the stomach and small intestine. We have not performed this laborious operation because under natural conditions the algae will be present both in the stomach and the small intestine.

Lovell and Sackey (1973) concluded that geosmin absorption is more rapid when fish are placed in tanks containing algae cultures than in tanks that receive glass wool filtered water from algae cultures because fish consume algae. Probably the filtered water contained a lower concentration of geosmin due to loss by adsorption onto the surface of glass wool (Danglot et al. 1983). To prevent earthy-flavor, which can be a problem in fish culture (Lovell and Sackey 1973; Iredale and York 1976), one needs to know where the flavor compound is absorbed. We conclude that geosmin is absorbed both from ingested algae and from geosmin in the water. Rainbow trout will only ingest algae accidentally with the feed, particularly when feed pellets are picked from the pond bottom. If trout are fed so that the feed is eaten before it reaches the bottom, the intake of algae will be reduced. We suggest that in this way it is possible to reduce the uptake of earthy-flavor compounds in rainbow trout so the absorption through the gastrointestinal tract will be of minor importance, and the major route of uptake will be absorption through gills and skin. As trout farms are flow-through systems, it is impossible to avoid earthy-flavor compounds if cyanophytes are present in the river or lake. The only way of controlling earthy-flavor in trout farming is to reduce the concentration of the earthy-flavor compound. If this is geosmin, we suggest that a lowering of pH of the water could reduce the concentration because geosmin is transformed by aqueous acid to the odorless argosmin (Gerber and Lechevalier 1965). Lovell (1983) showed that pH in natural waters influences the earthy-flavor in farmed channel catfish. In Danish trout farms receiving water from lakes, pH is lowered by adding hydrochloric acid to the inlet water during summer. This method of preventing earthy-flavor in farmed rainbow trout is not yet proven; experiments to do so should include tanks in which fish receive filtered water, simulating trout farms only receiving geosmin in the inlet water, and tanks containing algae, simulating trout farms with algae in the ponds.

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Method of Solving for Natural Mortality Rate for Stock Components with Different Schedules of Growth and Mortality

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Caddy, J. F. 1984. Method of solving for natural mortality rate for stock components with different schedules of growth and mortality. Can. J. Fish. Aquat. Sci. 41: 1226–1230.

A method is proposed for solving the natural mortality rates, M_A and M_B, for two stock components with different von Bertalanffy growth rates (K_A and K_B), where total mortality rates Z_A and Z_B are available for a series of years, and where the assumption of a constant M/K ratio can reasonably be made. The method has obvious applications for populations where the two sexes have different growth and mortality schedules, but have a constant relative availability to fishing.

On présente une méthode pour résoudre les taux de mortalité naturelle M_A et M_B de deux composantes du stock dont les taux de croissance (K_A et K_B) de von Bertalanffy diffèrent, quand les taux de mortalité totale Z_A et Z_B sont disponibles pour une série d'années et où l'on peut raisonnablement supposer un rapport M/K constant. Cette méthode possède des avantages évidents pour ce qui est des populations dans lesquelles les deux sexes ont des schèmes de croissance et de mortalité différents mais sont en constante disponibilité relative à la pêche.

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Estimation of natural mortality rate is notoriously difficult, especially after a fishery gets underway, and most direct methods of estimation (e.g. Silliman 1943; Paloheimo 1961) rely on a knowledge of total mortality rate Z and adjusted effort to extrapolate to mortality when only death due to natural causes prevailed. This approach (and, of course, direct estimation of natural death rate in the virgin population) makes the assumption that natural mortality rate M is invariant with fishing mortality rate F and, of course, that it remains constant during the fishable life span.

Other methods of estimation (e.g. Taylor 1962; Rikhter and Efanov 1976; Pauly 1980a) rely on generalizations concerning the relationship between M and other physiological and ecological parameters that have been demonstrated statistically for a range of stocks other than the one in question for which M is already known. As such, they may give perfectly valid results, but since they presuppose the existence of direct methods of estimation of M as a basis for generalization, they can be referred to as indirect methods of estimation.

Numerous situations exist where both mortality and growth rates differ between different stock components, but where the ratio M/K can be reasonably assumed constant. Examples where this is a reasonable assumption to make is for sympatric species in the species "flocks" found in some tropical lakes, e.g. the Tilapiine fishes of Lake Malawi (Trewavas 1983). However, the most obvious example here and the one principally addressed in this note is where growth and mortality rates differ between sexes. This is true, for example, in many decapod crustaceans, in cephalopods, and is commonly observed in many teleosts (e.g. the hakes, tunas, and flatfishes). Separate estimates of mortality and growth parameters by sex over a series of years should then suffice to provide direct estimates of M by sex.

Several ratio estimates for M using different assumptions were given by Sanders (1977) based on simultaneous solution of the familiar catch equation. Unless we wish to make fairly restrictive assumptions, however, namely that fishing mortality rates for females and males are the same (i.e. $F_F = F_M$), we require separate estimates by sex, of Z, t_c, and catch in numbers (C_N), and we need also to assume equal numbers of recruits $R_M = R_F$ before we can solve for M_M and M_F.

Methods

Basic assumptions — A simple method is proposed here that requires two basic assumptions, namely that a fishable population consists of at least two components with constant relative availability to fishing, for each of which we know the separate von Bertalanffy growth parameters K_A and K_B and the total mortality rates Z_A and Z_B for at least two periods, and preferably more, and that the ratio M/K is the same for the two components.

Within the accuracy of growth and mortality rate estimates in the literature this second assumption appears to be generally valid for species or even genera occupying the same environment and has been extended by Beverton and Holt (1959) to include members of the same family as well. Certainly, the M/K ratio is much less variable than either of the two component parameters considered separately. In the specific case of the two sexes occupying the same time–area strata a constant M/K ratio is a reasonably preliminary hypothesis to make in attempting to estimate mortality rates of stocks of species showing markedly different growth characteristics with sex. An exception here should be made for those species characterized by catastrophic mortality of one sex (after spawning, for example), where this method does not seem to apply.

Theory — Assuming then that M/K is a constant but unknown quantity, that we know K_F and K_M and $\bar{Z}_F$ and $\bar{Z}_M$ for a series of years, and noting that

$$F_M = Z_M - M_M$$

and

$$F_F = aF_M = Z_F - M_F$$

where a is the ratio of availabilities of males and females following full retention by the gear (assumed constant), then:

(1) $Z_F - M_F = a(Z_M - M_M)$.

Now if we assume (following Beverton and Holt 1966) that M/K is constant for a given genus or family, it would seem quite reasonable to assume that this applies also for the two sexes of a given species, especially for the same cohort sharing the same area–time stratum, i.e.

$$M_F = M_M(K_F/K_M),$$

then from equation (1):

$$a(Z_M - M_M) = Z_F - M_M(K_F/K_M)$$

giving

(2) $Z_F = M_M\,[(K_F/K_M) - a] + aZ_M$.

This can be solved by a functional regression of form

$$y = u + vx$$

where $\hat{a} = v$, and since $\hat{u} = M_M\,[(K_F/K_M) - \hat{a}]$,

$$\hat{M}_M = \frac{\hat{u}}{(K_F/K_M) - \hat{a}} \text{ and } \hat{M}_F = \hat{M}_M(K_F/K_M).$$

In practice it may not be possible to find realistic solutions for M's from all fits of regression equation (2), either because the underlying assumptions of the model are not being met or because errors/biasses in the measurement of Z's (or K's) were excessive.

These situations are evident upon drawing the functional regression line, if intercept u falls on the same side of the 45° line passing through the origin as point A ($y = \bar{Z}_F$, $x = \bar{Z}_M$: the arithmetic mean values for total mortality rate by sex for the data set). These situations are portrayed by line D–D in Fig. 1 and would imply that $Z_F > 0$ where $Z_M = 0$ and provides solutions for $M > Z$, which is unrealistic. Other situations not permitting a simple solution are, of course, a regression along the bisector C–C ($M_M = M_F$) and markedly curvilinear relationships, implying a change in underlying parameters with time.

Alternatively, if mean values of Z were estimated by sex for only two periods of years where fishing intensity had differed significantly (but the pattern of distribution of effort on males and females remains fairly constant), we could simultaneously solve pairs of equation (2) for M_M and hence also find M_F:

(3) ${}_1\bar{Z}_M a - M_M a = {}_1\bar{Z}_F - M_M(K_F/K_M)$

(4) ${}_2\bar{Z}_M a - M_M a = {}_2\bar{Z}_F - M_M(K_F/K_M)$

for the two stable periods of effort 1 and 2.

Confidence limits for the estimates of M_F *and* M_M — The functional regression approach of Ricker (1973) is commonly

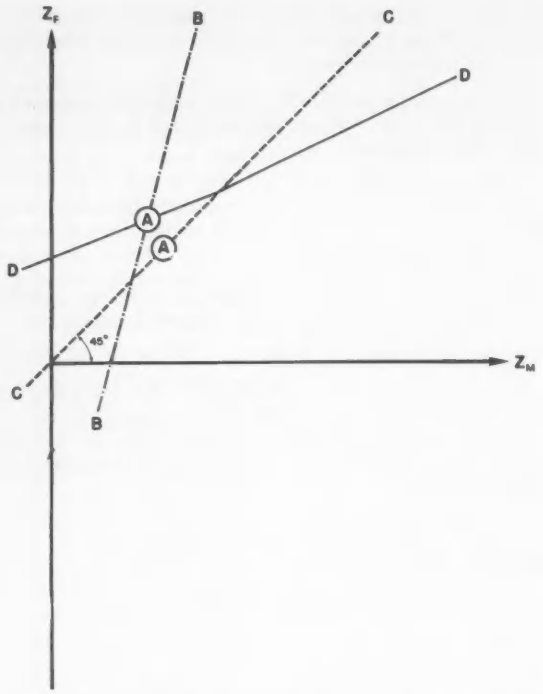

Fig. 1. Functional regression lines of paired mortality estimates for two population components $A + B$, solvable (line B–B) and not solvable (C–C and D–D), for M values by the present method. (Points A are the sample means $\bar{Z}_F$ and $\bar{Z}_M$.)

used by fisheries scientists in situations (e.g. in Paloheimo's method for M estimation) where it is unreasonable to consider Z_M or Z_F as either dependent or independent variables with respect to each other. This procedure has been criticized on a theoretical basis by some statisticians (e.g. Sprent and Dolby 1980), but the fact that it continues to be widely used by fisheries workers seems to point to some practical advantages. Thus, although employing the standard predictive linear regression is an alternative here, it is necessary to make a choice between the Z_F's and Z_M's as independent variables which give two solutions to the regression estimate. However, the range of these two predictive regression estimates may be an indication of the confidence that can be placed in the results. Alternatively, Ricker's approach to calculating confidence limits can be followed. This requires that the total variances of the Z's are in the ratio of their measurement variances. The parameters of the functional regression $y = u + vX$ can be easily obtained from the usual fitting routine for the predictive linear regression, noting that $v = b/r$ and $u = \bar{Y} - v\bar{X}$. Inspection of the plot of Z_y on Z_x should give some idea of the confidence to be placed in the estimate, which decreases with divergence of v and b values. More exactly, Ricker (1975) gave confidence limits for v or $v(\sqrt{B+1} \pm \sqrt{B})$, where $B = F(1 - r^2)/N - 2$ (F is the variance ratio) and where N equals the number of pairs of Z values and F is the variance ratio for $n_1 = 1$ and $n_2 = N - 2$ degrees of freedom.

Problems with calculating M's corresponding to both of these limits are likely to arise, especially for low values of M. In particular, unreal solutions to equation (2) are possible as discussed in relation to Fig. 1, where the resulting values of M obtained are greater than the observed annual values of Z. The practical solution in these cases appears to be to give the regression estimate of M and specify that it lies between zero and the upper bound, as calculated for some specified probability.

Estimation of mortality rates — Both of the above approaches to solving for M by sex imply that separate mortality rates are available and that some separate sampling for size and age by sex has been carried out. This would seem to be essential for those taxonomic groups where growth rates tend to differ between sexes (e.g. the hakes, flatfishes, and tunas), but in fact such data are rarely reported separately in the literature. Basic to the estimation of Z is either the use of one of the methods based on age composition analysis, such as the use of separate catch curves by sex (Ricker 1975; Robson and Chapman 1961), from which the mean Z can be determined from the slope of the right-hand line of the curve, or from the log ratio of successive age-classes in the combined age distribution for a number of years (the so-called stationary age frequency). Alternatively, one of the methods of estimating Z directly from separate size frequency data by sex can be used, again with the precondition that the size frequencies used are not biassed by the occurrence of better-than-average recruitment years. Among the possible methods can be mentioned a simple graphical method given in Jones (1981), which provides estimates of Z/K that can be converted to estimates of Z if growth rate is known.

Examples

Two examples follow of the method applied to flatfish species showing differentiation of growth rate with sex.

Example 1: Mean values of Z from a series of catch curves by sex — Estimates of M for American plaice (*Hippoglossoides platessoides*) were obtained by Pitt (1972) from adjacent divisions of ICNAF (3L + 3N) where age compositions had been determined separately for males and females. From these, annual average values of $\bar{Z}_t$ were obtained by fitting a straight line to the right-hand size (RHS) of separate catch curves for each year. Estimating Z's for single years of data evidently contributed significantly to the variance of estimates of Z obtained in this way, but for both divisions, $Z_F \geqslant Z_M$ (Table 1).

The above mortality values were used by Pitt (1972), together with annual effort data, to estimate M separately by sex using the methods of Beverton and Holt (1957) and Paloheimo (1961). Variance was high, and he had to discard a number of anomalous values. Considering the relatively high longevity of the species, his estimates of M_M of the order of 0.25 and M_F of around 0.2 seem reasonable.

Using the present method, separate pairs of values of $\bar{Z}$ by sex were pooled for both divisions, and only one pair of values was discarded (for 3L in 1946 where Z_F is half the value of any of the other eight annual values of Z_F in the series). Values of Z_F and Z_M are plotted in Fig. 2.

This species shows a clear divergence of growth in length with sex, and in a closely adjacent area, Pitt (1978) gave values of $K_M = 0.14$ and $K_F = 0.11$.

A functional regression was fitted to data from Table 1 of

TABLE 1. Estimates of Z by sex from separate catch curves by age for American plaice from ICNAF divisions 3L and 3N (Pitt 1972). Values in parentheses not used.

Year	Z_M	Z_F
Division 3L		
1943	0.43	0.43
1944	0.39	0.50
1945	0.50	0.53
(1946)	(0.22)?	(0.63)
1947	0.44	0.56
1948	0.62	0.66
Division 3N		
1947	0.42	0.53
1948	0.56	0.72
1949	0.52	0.71

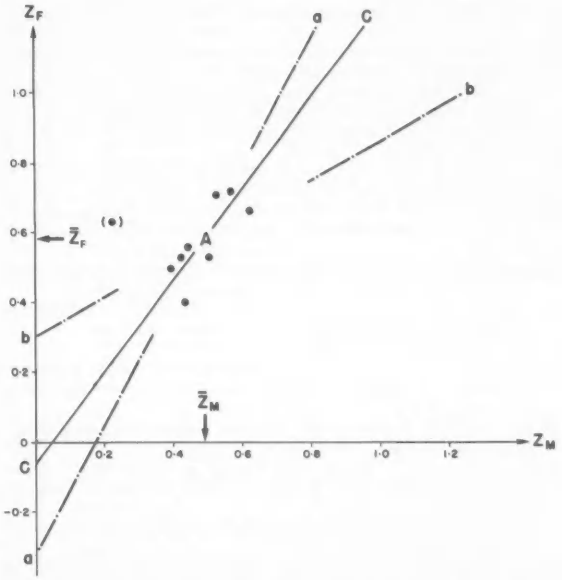

FIG. 2. Functional regression line (C–C) of $\bar{Z}_F$ on $\bar{Z}_M$ for American plaice, ICNAF divisions 3L and 3N (1946 point (●) omitted). Lines a–a and b–b represent the confidence limits for the slope of the regression.

form

$$\bar{Z}_F = u + v\bar{Z}_M$$

which gave $u = -0.065$ and $v = 1.331$. Thus, $\hat{a} = 1.331$, and since $K_F/K_M = 0.786$,

$$\hat{M}_M = \frac{-0.065}{0.786 - 1.331} = 0.119$$

$$\hat{M}_F = \frac{\hat{M}_M \cdot K_F}{K_F} = 0.094.$$

These values are rather lower than those obtained by Pitt (1978), but not much so, and seem reasonably in line with the high longevity of the species (20+ yr). Since the method described here provides values of M that presumably correspond to exploited conditions, this slight discrepancy may also be understandable, since M's under exploitation may be slightly lower.

Confidence interval for the estimate — For sample size $N = 8$, $R^2 = 0.604$, and the variance ratio for degrees of freedom $n_1 = 1$ and $n_2 = 6$ was obtained from Steel and Torrie (1960, table A.6) for $P = 0.05$.

Confidence limits for the slope v of the regression were 0.553–1.809, and equation (2) was solved for $\bar{Z}_M = 0.485$, $\bar{Z}_F = 0.580$, to give corresponding limits for M_M. That for $v = 1.809$ (line a–a in Fig. 2) gave $M_M = 0.290$ and $M_F = 0.228$; that for $v = 0.553$ (line b–b in Fig. 2) gives an unreal solution, resultant values of $M_M = 1.339$ and $M_F = 1.052$ being obtained. In this situation, it would seem safer to conclude that the estimated values of M_M lie between 0 and 0.29 and for M_F between 0 and 0.228.

Example 2: Solution of simultaneous equations for M *and* a — Tremblay and Axelsen (1980) gave some preliminary age compositions and catch curves for two separate years for a stock of Greenland halibut (*Reinhardtius hippoglossoides*) in the Gulf of St. Lawrence separately by sex. Apparently the fishery has been in the course of rapid development during the period of observation, and 2 yr of data almost certainly is inadequate for proper estimation of M's by simultaneous equations, given that the assumptions of Silliman's (1943) method would be more appropriate, namely two periods of steady fishing at different F's. However, the data do serve to illustrate the method, but the results should be treated with caution.

The above authors provided estimates of $K_M = 0.088$ and $K_F = 0.048$ ($K_F/K_M = 0.545$) and separate estimates of $Z^{78}{}_M = 0.43$, $Z^{78}{}_F = 0.35$, $Z^{79}{}_M = 0.56$, and $Z^{79}{}_F = 0.50$ from catch curves.

Substituting in equations (3) and (4) and subtracting:

1978:

(5) $0.43a - M_M a = 0.35 - M_M\,(0.545)$

1979:

(6) $0.56a - M_M a = 0.50 - M_M\,(0.545)$

$$-0.13a = -0.15$$

$$a = 1.154.$$

Substituting in equation (5) and solving for M_M:

$$M_M = 0.24$$

$$M_F = \frac{K_F \cdot M_M}{K_M} = 0.545 \times 0.086.$$

Therefore, $M_F = 0.13$.

These values are not out of line given the low growth rates and the low temperatures of the environment (3–6°C). The values predicted by the equation of Pauly (1980b), which gives $\log_{10} M$ as a function of K, L_∞ ($L^M{}_\infty = 93.4$ cm; $L^F{}_\infty = 138.3$ cm), and mean annual ambient temperatures (taken as 4.5°C), are somewhat lower ($M_M = 0.114$, $M_F = 0.069$) but reasonably close. No confidence limits are provided here, and these values are simply meant to illustrate the methodology.

Discussion

One of the main problems likely to be encountered in applying this method is the combination of a relatively limited range of Z values and the general imprecision of most estimates of Z, meaning that the ellipse of points around the functional regression is likely to be compressed along its axis, making for wide confidence limits, and suggesting that data for all years from the start of the fishing to full exploitation will need to be included.

As noted, not all solutions for M will be feasible ones, and inspection of the plotted regression and points helps in the detection of unreal solutions. Checking the resultant values with a general method such as that of Pauly (1980a) should provide a control against adoption of unreal solutions. This problem of estimation, and in particular, determining unreal confidence limits, is shared by all other methods of estimating M, hence the general absence of confidence intervals calculated for this important parameter. However, this new method does estimate values of M for the exploited stock directly, rather than extrapolating to unexploited conditions, as with other classical approaches, and it is suggested that if annual recruitment of, for example, males and females is correlated, the impact of recruitment variations described by Ricker (1975) on catch curve estimates of Z (which are later compared) may be reduced.

The feasibility of using the assumption of constant M/K in estimating values of M separately by sex prompts the questions of whether this method can be extended to situations where the assumption of a common M/K value can still reasonably be made, i.e. where two separate groups of animals can be recognized in a common fishery, with divergent growth rates, a constant relative availability, and some way of obtaining a series of separate annual estimates of Z.

Two cases that may merit further exploration are mentioned here without examples:

(i) A species showing no difference in growth rate with sex, but where individually recognizable growth forms occur within the range of the fishery. The possibility of estimating M separately then exists if these groups of individuals suffer a constant ratio of fishing intensities and if K values are known for the two or more "substocks."

(ii) Two or more species of the same genus or family having different growth rates, K_A and K_B, occurring in the same multispecies fishery, with constant relative availability. A series of values exist for Z_A and Z_B in successive time periods, and the assumption of Beverton and Holt (1966) of constant M/K for taxonomically related species is believed to be valid. The method may then provide separate values of M for each species based on annual values of Z by species. This may have particular application for species "flocks" in highly diverse multispecies tropical fisheries.

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Selective Predation for Vertebral Number of Young Sticklebacks, *Gasterosteus aculeatus*

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Young laboratory-reared threespine sticklebacks, *Gasterosteus aculeatus*, were exposed to predation by pumpkinseed sunfish, *Lepomis gibbosus*, until 50–65% of the initial number were eaten; vertebral counts of survivors were compared with those of unexposed controls. Experiments were conducted on prey of two different mean sizes and at two temperatures. With smaller prey (average initial length 8.2 mm), selective predation for vertebral number was striking; survival rate was from 1.3 to 1.7 times greater for fish with 31 vertebrae than for those with 32. With larger prey (average initial length 8.9 mm), experimental and control fish did not differ significantly in vertebral number. Selection did not vary significantly with water temperature; each prey length was tested at 15°C and 17 or 20°C. Selectivity of predation with respect to vertebral number was not attributable to selection with respect to body size of prey.

De jeunes épinoches à trois épines, *Gasterosteus aculeatus*, élevées en laboratoire ont été soumis à la prédation par des crapets-soleil, *Lepomis gibbosus*, jusqu'à ce que de 50 à 65 % des épinoches aient été mangées. Le nombre de vertèbres des épinoches survivantes a été comparé à celui de témoins. Les essais ont porté sur des proies de deux tailles moyannes différentes et ont été effectués à deux températures. La prédation sélective quant au nombre de vertèbres est frappante chez les proies les plus petites (longueur moyenne initiale de 8,2 mm), le taux de survie étant de 1,3 à 1,7 fois supérieur chez les poissons à 31 vertèbres comparativement à ceux à 32 vertèbres. Le nombre de vertèbres ne différait pas de façon significative entre les poissons d'essai et les témoins chez les individus plus gros (longueur moyenne initiale de 8,9 mm). La sélection ne présentait pas de variations significatives en fonction de la température de l'eau ; des essais à 15°C et à 17 ou 20°C ont été effectués avec des proies des deux longueurs). La sélectivité de la prédation quant au nombre de vertèbres ne s'expliquait pas par une sélection portant sur la taille des proies.

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Surprisingly wide variation in vertebral number is commonly found within wild fish populations. The "neutralist" view has been that such variation persists because the precise vertebral count is without selective significance (Fowler 1970). Wide malleability of vertebral count in response to environmental influences during early development (Lindsey and Arnason 1981) is also consistent with a lack of strong selective advantage to particular counts. However, a contrasting "selectionist" view is supported by the widespread tendency among related forms for higher vertebral number to be associated with longer maximum body length ("pleomerism") and with higher latitude or colder waters ("Jordan's rule") (Lindsey 1975). That locomotory performance may be functionally related to vertebral number is also suggested by hydrodynamic models (Spouge and Larkin 1979). We describe here experiments in which young threespine sticklebacks, *Gasterosteus aculeatus*, are exposed to predation by pumpkinseed sunfish, *Lepomis gibbosus*, as a test of the hypothesis that the precise vertebral count is without functional significance.

Material and Methods

Breeding sticklebacks were collected from Kennedy Lake on Vancouver Island, B.C. Each male was artificially crossed with two females, and their offspring were reared in the laboratory. For each of three experiments, the offspring of a single collection of parents (about 25 males and 50 females) were mixed and distributed among six 190-L tanks, 15–20 d after hatching. Two tanks were designated as control tanks and four as experimental tanks. One control and two experimental tanks were maintained at 15°C; the remaining tanks were maintained at either 17 or 20°C. Tanks were illuminated by overhead fluorescent lights on a photoperiod of about 16.5 h light : 7.5 h dark. Water in-flow per tank was about 1–2 L/min. Cover was usually provided by shredded plastic suspended near each end of experimental tanks but was removed while assessing the extent of predation and was usually not replaced when the estimated number of fry eaten approached the desired number. The proportion of time during which cover was available thus varied among tanks and experiments but was unrelated to the selectivity of predation. After about 15 h of acclimation, sticklebacks in experimental tanks were exposed to predation by 10–30 sunfish for 10–50 h until 50–60% of the initial number had been eaten. Sunfish were removed overnight in experiments lasting more than 1 d. The sunfish used were collected from Holden Lake, Vancouver Island (which also contains sticklebacks), and averaged 24 mm in standard length (range 15–30 mm).

Fry were preserved in 10% buffered formalin, stained with alcian blue, cleared with trypsin and 0.5% KOH, and stored in glycerin. Counts were made of centra, excluding the urostyle.

TABLE 1. Vertebral counts of sticklebacks exposed (experimental) or unexposed (control) to predation by sunfish. Probability values test for partial association between vertebral count and predation treatment.

Exp.	Treatment	Temp. (°C)	% eaten	No. surviving	Standard length of survivors (mm)		Vertebral count (%)					Probability
					Mean	SD	29	30	31	32	33	
1	Control	15	0	87	8.07	0.52		1.1	41.4	56.3	1.1	
		20	0	89	8.55	0.72			40.4	59.6		
												0.0064
	Experimental	15	62	106	8.23	0.51		1.9	55.7	40.6	1.9	
		15	55	127	8.26	0.59			52.8	44.9	2.4	
		20	61	123	8.52	0.61		1.6	52.8	44.7	0.8	
		20	64	107	8.74	0.54		0.9	54.2	43.9	0.9	
2	Control	15	0	126	8.14	0.72		6.3	47.6	45.2	0.8	
		20	0	117	8.23	0.66		5.1	46.2	47.0	1.7	
												0.026
	Experimental	15	58	144	8.50	0.64		6.9	59.0	33.3	0.7	
		15	60	132	8.48	0.69	0.8	8.3	49.2	39.4	2.3	
		20	51	165	8.43	0.68		3.0	52.7	43.0	1.2	
		20	51	167	8.58	0.75		6.0	52.7	40.7	0.6	
3	Control	15	0	132	8.91	0.82		4.5	48.5	47.0		
		17	0	152	8.93	0.84		4.6	57.2	36.8	1.3	
												0.27
	Experimental	15	58	162	9.17	0.54		4.3	60.5	34.6	0.6	
		15	63	147	9.10	0.55		4.8	54.4	39.5	1.4	
		17	53	187	9.03	0.64		2.1	57.2	40.1	0.5	
		17	59	157	9.10	0.50		1.9	56.1	38.9	3.2	

For each experiment, we calculated the probability that the partial association between vertebral count and predation treatment is zero, using data grouped as fish with 31 or fewer vertebrae or fish with 32 or more. This probability is given by the difference in likelihood ratio chi-square (G^2) between the following log-linear models:

$$\ln F_{ijk} = \theta + \lambda^R{}_i + \lambda^V{}_j + \lambda^P{}_k + \lambda^{RV}{}_{ij} + \lambda^{RP}{}_{ik} + \lambda^{VP}{}_{jk}$$

and

$$\ln F_{ijk} = \theta + \lambda^R{}_i + \lambda^V{}_j + \lambda^P{}_k + \lambda^{RV}{}_{ij} + \lambda^{RP}{}_{ik}$$

where F_{ijk} is the expected frequency in the cell (i, j, k) and λ is the main or interaction effect indicated by its superscript. The superscripts V, P, and R refer to vertebral count class, predation treatment, and replication, respectively. All cells in replications 3 and 4 of the control treatment were defined as "structural zeros." Probabilities were calculated using the computer program BMDP4F (Dixon 1981). Correlations between vertebral count and length were calculated using program BMDP1R (Dixon 1981).

Results

Vertebral count distributions were apparently homogeneous among tanks before exposure to predators. In each of the first two experiments, distributions in the two control tanks were virtually identical (Table 1). Differences between the control distributions in the third experiment were not statistically significant ($p > 0.1$, according to a chi-square test).

The first two experiments produced striking evidence of selective predation with respect to vertebral number (Table 1). The frequency of fish with 31 vertebrae was consistently greater in experimental than in control tanks after predation. Judging from the difference in counts between control and experimental groups, the survival rate of fish with 31 vertebrae was about 1.7 and 1.3 times that of fish with 32 vertebrae in the first and second experiments, respectively.

The third experiment differed from the previous two in average prey size; judging from the size distributions of control and experimental groups, the majority of fish eaten were about 8.5–10.5 mm long, whereas most of those eaten in the first two experiments were about 7.0–8.5 mm long. Predation on these longer fish was not significantly selective for vertebral number; the frequency of fish with 31 vertebrae was only slightly greater in experimental than in control tanks.

Predation was also selective with respect to prey size. The average length of fish surviving predation in experimental groups was usually slightly greater than that of fish unexposed to predation in the corresponding control groups (Table 1). Vertebral number and length were directly correlated among fish in all control groups, but this relationship was not significant ($p = 0.12$ in the first experiment, $p = 0.59$ in the second, and $p = 0.22$ in the third) and, moreover, was in the direction that would cause size selective predation to counteract rather than contribute to the observed differences in vertebral numbers. Therefore, selectivity of predation with respect to vertebral number cannot have been due to size selection in these experiments.

No significant effect of temperature on the extent of selective predation was detected. Vertebral counts of survivors in experimental groups were virtually identical between temperatures in experiment 1. In experiments 2 and 3, counts were slightly higher in experimental groups at the higher temperature, but differences between temperatures were not statistically significant ($p = 0.20$ and 0.37, respectively, according to

chi-square tests using data grouped as above) and may simply reflect the lower percent mortality at the higher temperatures.

Discussion

Our results demonstrate that predation is strongly selective for vertebral number in some circumstances. This selection cannot be attributed to size selection by predators. However, it might result from a correlation between vertebral number and some other morphological or behavioural character of importance in avoiding predators. At the sizes used here, few other morphological characters likely to be of importance in avoiding predators are yet expressed; lateral plates are not yet formed, spines are rudimentary or undeveloped, and fin rays are not fully formed. Behavioural differences related to vulnerability to predation have been found between different lateral plate phenotypes in sticklebacks (Moodie et al. 1973) but the different phenotypes were from different populations. The sticklebacks used here were probably from a single population, so such associations between traits are less likely. Extremely strong selection with respect to correlated characters would have to be proposed to account for our results. Difference in locomotory performance between fish with different vertebral numbers seems to be a more likely factor in the selective predation we report. Such differences could be related to flexibility or to myomere number, or to some other feature of the axial segmentation (Lindsey 1975).

Lindsey (1975) suggested that pleomerism might arise because of a functional correlation between body size and optimum number of segments. Our results are consistent with such an explanation, in that fish with lower vertebral counts were at an advantage at shorter lengths (7.0–8.5 mm) but not at slightly longer lengths (8.5–10.5 mm). We also suggest that the critical sizes to which vertebral number is adapted are those of the early free-swimming stages, at least in sticklebacks. However, more experiments at a wider range of sizes are needed to fully address these questions.

A functional reason may also be sought for Jordan's rule. Water viscosity, which is dependent on temperature, is a parameter in hydrodynamic calculations and has been implicated in Jordan's rule (Aleev 1969; Spouge and Larkin 1979). We failed to detect an effect of temperature on the extent of selective predation, but experiments over a wider temperature range are needed.

Our results indicate that precise vertebral number is not always selectively neutral. Why then is there so much vertebral variation in natural populations? Possibly, variation in vertebral number within populations is maintained because of year-to-year variation in the body length or the environmental conditions at which selection is most stringent. Variation is maintained in fish both by genetic and by environmentally induced mechanisms. The latter may be adaptive if the environmental factors affecting counts during embryo development are correlated with factors that later determine which count is best when the larvae are free-swimming.

By demonstrating that fish with different vertebral numbers are subject to different selection pressures, we suggest that in each year-class the mean vertebral count of survivors may be expected to shift with time. Tester (1937) did in fact observe a small but apparently significant increase in the mean vertebral count of year-classes of British Columbia herrings (*Clupea pallasi*) with age, and he suggested the possibility of differential mortality with respect to vertebral count. Fisheries managers should be aware of this possibility when using vertebral or other meristic characters to delineate exploited stocks of fishes.

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Forecasting Yields of Two-Sea-Winter Atlantic Salmon (*Salmo salar*) from Icelandic Rivers

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Scarnecchia, D. L. 1984. Forecasting yields of two-sea-winter Atlantic salmon (*Salmo salar*) from Icelandic rivers. Can. J. Fish. Aquat. Sci. 41: 1234–1240.

To forecast yields of two-sea-winter Atlantic salmon (*Salmo salar*) from 15 Icelandic rivers, I developed predictive regression equations based on yields of grilse of the same smolt class harvested in the previous year. The relationships were positive and significant ($P < 0.05$) for all rivers. The logarithm of grilse catch explained 25–85% of the variation in logarithm of two-sea-winter salmon catch the following year. Inasmuch as statistical tests for linearity between the variables were difficult to interpret and showed conflicting conclusions, I consider them inadequate for assessing whether density dependence occurs between grilse and two-sea-winter salmon. Linear or near linear relationships, which imply no density dependence, appear to occur between log grilse and log two-sea-winter salmon yields. The critical period determining run size from a given escapement thus occurs either during the freshwater rearing phase or during the first year the salmon are at sea.

Afin de prédire les rendements du saumon de l'Atlantique (*Salmo salar*) ayant passé deux hivers en mer et peuplant 15 rivières d'Islande, l'auteur a mis au point des équations de régression pour l'extrapolation basées sur les rendements de madeleineaux appartenant à la même classe de saumoneaux et pêchés l'année précédente. Pour toutes les rivières, les relations étaient positives et significatives ($P < 0{,}05$). Le logarithme de la prise de madeleineaux expliquait dans une proportion de 25 à 85 % la variation du logarithme de la prise, l'année suivante, de saumon ayant passé deux hivers en mer. Puisque les tests statistiques de la linéarité entre les variables étaient difficiles à interpréter et généraient des conclusions opposées, l'auteur les considèrent comme inadéquates pour déterminer s'il existe une dépendance relative à la densité entre les madeleineaux et les saumons ayant passé deux hivers en mer. Des relations linéaires ou presque linéaires, qui ne dénotent aucune dépendance par rapport à la densité, semblent exister entre les rendements (log) des madeleineaux et des saumons ayant passé deux hivers en mer. La période critique qui détermine l'importance de la remonte à partir d'une échappée donnée a donc lieu soit pendant la phase de croissance en eau douce, soit pendant la première année de vie en mer.

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If fishery managers can forecast how many salmon of a particular stock will be available to a fishery before the fishing season, they can adjust harvest rates to provide adequate escapement, and fishermen can allocate their labor and capital in accordance with anticipated fishing success.

One approach to forecasting the yield and escapement of anadromous salmonids (*Salmo* sp. and *Oncorhynchus* sp.) is based on the yield and escapement of fish of the same smolt class that returned to the rivers the previous year. For Atlantic salmon (*S. salar*), this approach usually involves estimating the projected combined yield and escapement of two-sea-winter salmon from the yield and escapement of grilse the year before. Since Atlantic salmon escapement is seldom known, biologists often assume a constant or abundance-dependent harvest rate, or a constant effort between years, and then predict the anticipated yield for a given amount of fishing effort. With such a method, the abundance of two-sea-winter salmon can sometimes be predicted accurately.

This forecasting method has a long history. Jacobsson and Johanssen (1921), who summarized catch data for Atlantic salmon from the Frisenvold Weir on the Gudenaa River, Denmark, wrote:

> The summer salmon consists mainly of two groups: Group A, which spawn ca. 18 months after the migration to the sea [grilse], ... and Group B, the spawning time of which occurs ca. 2-½ years after the migration to the sea [2 sea-winter salmon] ... We have been able to distinguish between salmon of Group A and salmon of Group B ... by means of ... the size of the specimens and by an investigation of the scales of a smaller group of specimens ... It will be seen ... that from a certain year will partly originate A-salmon 3 years later, partly B-salmon 4 years later, and ... an obvious connection exists between the number of A-salmon in a certain year and the number of B-salmon in the following year ... If we investigate ... the correlation between the catch anomalies for A-salmon in one year and ... B-salmon the following year in the period 1899–1913, ... the calculation ... shews [*sic*] that we, with a considerable certainty, can predict that if relatively many A-salmon are caught in a certain year, relatively many B-salmon will be caught in the following year, and that a small catch of A-salmon will be followed by a small catch of B-salmon the following year.

This fundamental method of prediction has been used for

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TABLE 1. Correlation coefficients between grilse catches and two-sea-winter salmon catches the following year, coefficients of variation in grilse catches, and results of density dependence tests for 15 Icelandic rivers (*$p < 0.05$; **$p < 0.01$).

River	Correlation coefficients			Coefficients of variation for grilse catches[a]	Density dependence (Morris test, $P < 0.05$)[b]
	Residual degrees of freedom	Untransformed	Log-transformed		
Laxá í Kjós	23	0.59**	0.53**	0.30	Yes
Laxá í Leirársveit	19	0.68**	0.66**	0.47	Yes
Laxá í Dölum	33	0.71**	0.55**	0.56	Yes
Fáskrúd	31	0.66**	0.61**	0.51	Yes
Langadalsá	17	0.87**	0.86**	0.56	No
Hrútafjardará	17	0.75**	0.82**	0.54	Yes
Vesturá	23	0.74**	0.84**	0.53	No
Núpsá	23	0.56**	0.68**	0.54	Yes
Austurá	23	0.78**	0.89**	0.71	Yes
Midfjardará	23	0.79**	0.87**	0.55	Yes
Vídidalsá	20	0.52*	0.50*	0.46	Yes
Vatnsdalsá	18	0.81**	0.74**	0.64	Yes
Laxá á Ásum	21	0.74**	0.82**	0.51	No
Vesturdalsá	22	0.93**	0.88**	0.74	No
Hofsá	20	0.87**	0.92**	0.78	No

[a]From Scarnecchia (1984).
[b]Varley–Gradwell tests showed no density dependence for any of the 15 rivers.

various salmon stocks since then with only minor statistical modifications. In Oregon, Gunsolus (1978) predicted returns of mixed stocks of coho salmon (*O. kisutch*) from returns the previous year of precocious males ("jacks"). Peterman (1982) improved forecasts of abundances of several North American stocks of sockeye salmon (*O. nerka*) by using functional regressions (Ricker 1973) and by transforming the data to natural logarithms. Because of the strong linear correlations between abundance of returning fish of a given smolt class in one year and the abundance of returning fish of the same smolt class in the following year, Gunsolus (1978) and many others have argued that if salmon suffer density-dependent mortality at sea, it most likely occurs soon after the smolts enter the sea, rather than later when the salmon are large.

In Iceland, river owners and managers want to know how many two-sea-winter salmon will return to the rivers, anglers want to accurately forecast the quality of fishing for two-sea-winter salmon the following year, and salmon ranchers want to forecast the number of two-sea-winter fish that will be returning to their smolt release sites. Biologists and salmon ranchers also wish to know if density-dependent mortality acts on salmon between the grilse stage and the two-sea-winter salmon stage. Kristjánsson (1982) first documented the close relation between yield of grilse in one year and yield of two-sea-winter salmon the next year for three northeastern Icelandic rivers. In this paper, I extend his work to several other stocks, modify and extend the statistical analyses, and include earlier yield data.

My objectives were to develop predictive regression equations for yield of two-sea-winter salmon for 15 Icelandic stocks of Atlantic salmon and to make inferences about density dependence between the grilse and two-sea-winter salmon stages.

Methods

Since no long-term escapement data were available by smolt class for Icelandic rivers, all relations analyzed were based on yields. For 15 rivers (see Scarnecchia 1984 for locations), I determined annual yield of salmon of each smolt class from actual counts of salmon caught by anglers. Weight and sex of each salmon had been recorded when captured. For each year's data, yields of grilse and two-sea-winter salmon (sexes combined) were computed with the aid of weight–frequency distributions. Scales from a few stocks were also read to clearly define the weight at which grilse and two-sea-winter salmon should be separated (Jacobsson and Johansen 1921; Scarnecchia 1983). Three-sea-winter salmon were not considered because they were scarce on most rivers. Catch on Midfjardará was the sum of catches on its tributaries Vesturá, Núpsá, and Austurá, plus lower river fish from all three stocks.

There is no significant fishery in the ocean by Icelanders (Ísaksson 1980) that would bias catches in the rivers, although the effects of the Greenland and Faroese fisheries on the stocks remain largely unknown. Nominal fishing effort on 12 of the 15 rivers was nearly constant over the period of study (Scarnecchia 1984); however, effective effort may have increased in recent years if the higher cost of permits induced more aggressive angling. I assumed that changes in fishing were slight between adjacent years, even though moderate effort changes may have occurred between the earliest and latest years considered in the study.

Relations between grilse catches in one year and two-sea-winter salmon catches the next year were computed for both untransformed and logarithmically transformed data with predictive linear regressions (Snedecor and Cochran 1967). To evaluate whether the observed logarithmically transformed relations deviated from linearity, I used a two-tailed t statistic to test if the slopes of the log–log relations were equal to 1 (Morris 1959); I also used the Varley–Gradwell test described by Southwood (1978). The tests were two-tailed, because I believed that either negative density dependence (increased mortality) or positive density-dependence (delayed maturation) could occur. I attempted to determine how well the two regression assumptions of homoscedasticity and normality of residuals were met. Homoscedasticity was tested with Kendall's (1955) Tau statistic by plotting absolute values of

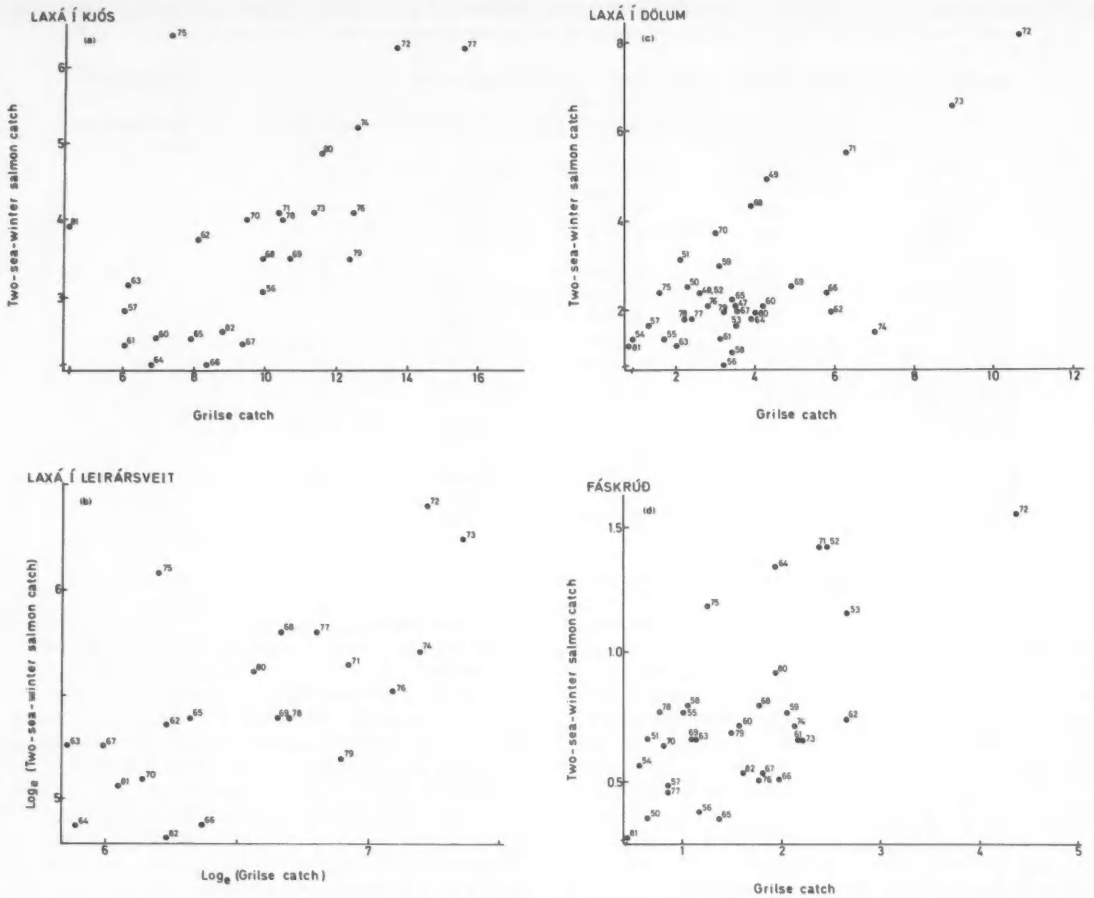

FIG. 1. Relations between yield of two-sea-winter salmon and yield of grilse the previous year for various Icelandic rivers. Year of two-sea-winter salmon catch (e.g. 61 = 1961) is marked on the graphs. (a) Catches on Laxá í Kjós (hundreds of fish); two-sea-winter catch = 0.278(grilse catch) + 109.127. (b) Log catches on Laxá í Leirársveit; log (two-sea-winter catch) = 0.640 log (grilse catch) + 1.278. (c) Catches on Laxá í Dölum (hundreds); two-sea-winter catch = 0.535(grilse catch) + 62.083. (d) Catches on Fáskrúð (hundreds); two-sea-winter catch = 0.265(grilse catch) + 33.140.

residuals against the independent variable (Peterman 1982). Normality of residuals was tested with the Kolmogorov–Smirnov one-sample goodness-of-fit statistic. Statistics were computed with the aid of the *Statistical Package for the Social Sciences* (Nie et al. 1975; Hull and Nie 1981).

Results

For 14 of the 15 rivers, there were highly significant ($P < 0.01$) positive relations between the catch of grilse in one year and the catch of two-sea-winter salmon in the following year. For the remaining river, Vídidalsá, the relations were also significant, but at $P < 0.05$ (Table 1; Fig. 1). The relations for logarithmically transformed data were slightly stronger or weaker for various cases, but their statistical significance at the 0.01 and 0.05 levels remained unchanged (Table 1). Depending on the river, log grilse catch explained from 25 to 85% of the log catch of two-sea-winter salmon in the next year. For some rivers (e.g. Laxá í Kjós, Fig. 1a), the relation improved markedly if anomalous data for one year were removed. For only one of the rivers, Laxá á Ásum, did the ratio of grilse (t) to salmon ($t + 1$) change significantly ($P < 0.05$) over the time periods investigated; in this river, significantly fewer grilse were caught relative to older salmon in recent years than in earlier years.

Of the 15 relations for the log-transformed data, 10 were significantly different from linear as judged by the Morris test; none were judged different from linear with the Varley–Gradwell test (Table 1).

The variances of some of the catches were stabilized by transforming the data to natural logarithms. Untransformed data from six rivers resulted in significantly ($P < 0.05$) positively heteroscedastic relations, but after transformation, only three were heteroscedastic, one of which was previously homoscedastic but became negatively heteroscedastic (Table 2). All residuals were normally distributed for both untransformed and logarithmically transformed data.

Discussion

Since no long-term escapement data are available for any of

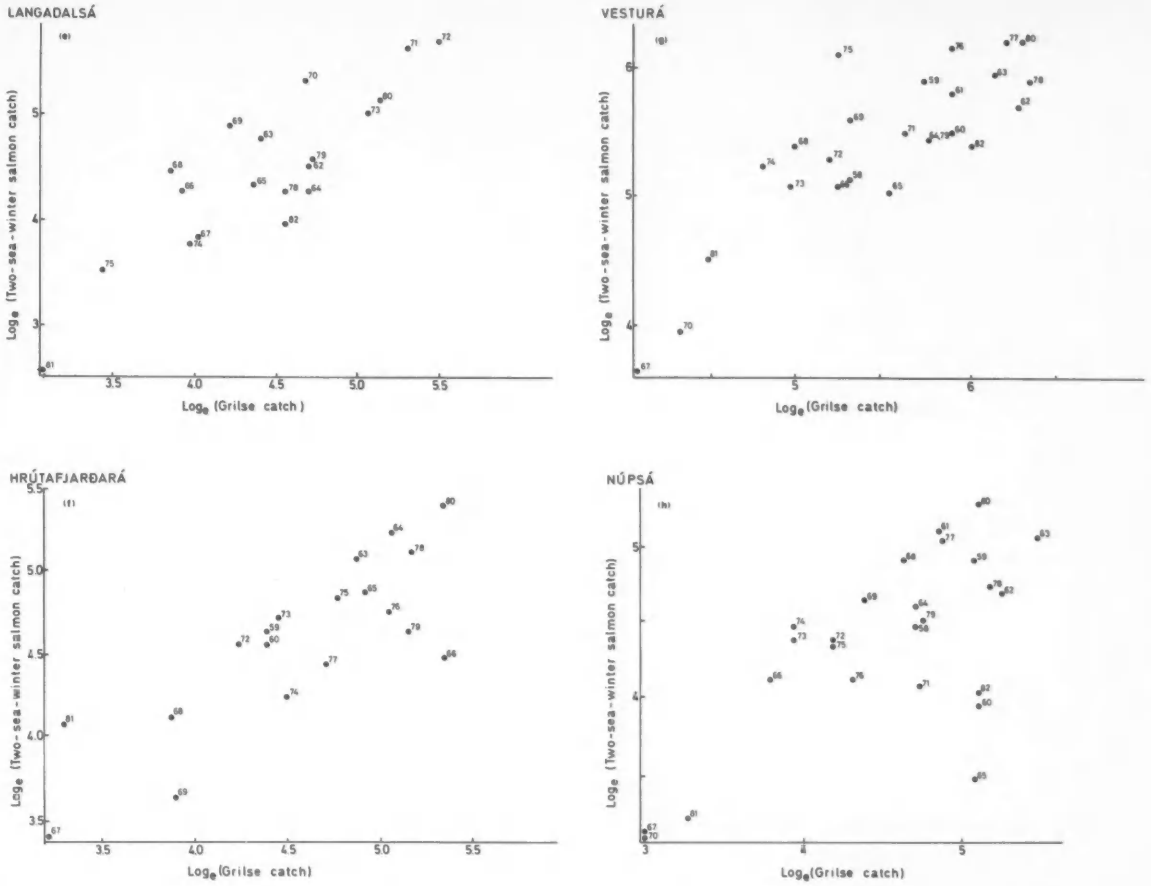

FIG. 1 (*Continued*). (e) Log catches on Langadalsá; log (two-sea-winter catch) = 1.095 log (grilse catch) − 0.418. (f) Log catches on Hrútafjardará; log (two-sea-winter catch) = 0.660 log (grilse catch) + 1.553. (g) Log catches on Vesturá; log (two-sea-winter catch) = 0.878 log (grilse catch) + 0.581. (h) Log catches on Núpsá; log (two-sea-winter catch) = 0.605 log (grilse catch) + 1.639.

the 15 rivers, I cannot ascertain if the relations between total abundance of grilse and two-sea-winter salmon are linear. Although the relation between harvest rate and total abundance need not be constant, linear, or nearly linear relations exist between yields of grilse and of two-sea-winter salmon for these rivers, at least over the observed ranges of catches. The widely differing conclusions on density dependence obtained from use of the Morris and the Varley–Gradwell methods do not clarify whether linear relations exist. Southwood (1978) and Benson (1973) discussed the controversies and problems surrounding the tests; Peterman (1978) found large discrepancies between the conclusions depending on which test he used. For the Icelandic data, the discrepancies between tests and difficulties in interpretation make them of little value for assessing the presence or absence of density dependence.

If significant density-dependent mortality occurs at sea, studies of Atlantic salmon (Jacobsson and Johansen 1921; Kristjánsson 1982; this paper), coho salmon (Gunsolus 1978) and sockeye salmon (Peterman 1982) indicate that it must occur mainly during the first year the salmon are in the sea. The critical period determining run size must also be during the freshwater rearing phase or during the first year the fish are at sea.

Although Peterman (1982) found that log transformations substantially improved stability of variance and normality of residuals for several stocks of Pacific salmon, I found that the benefits of log transformations of the Icelandic data ranged from moderate to nil, depending on the stock. For these data, a log transformation should not necessarily be preferred over untransformed data, since the data may be overtransformed (e.g. to negative heteroscedasticity) in searches for higher correlation coefficients.

The closest linear fits between log-transformed grilse and two-sea-winter salmon were for the northern rivers Austurá, Hofsá, and Vesturdalsá, which showed the three highest annual variations in grilse catches (Table 1). Variations in grilse catches were lower and correlations between grilse and two-sea-winter salmon yields were poorer in Vídidalsá, as well as in the southwestern rivers Laxá í Kjós and Laxá í Leirársveit. The better predictive fits for the northern rivers apparently result in part from the instability in their annual yields, which produces a

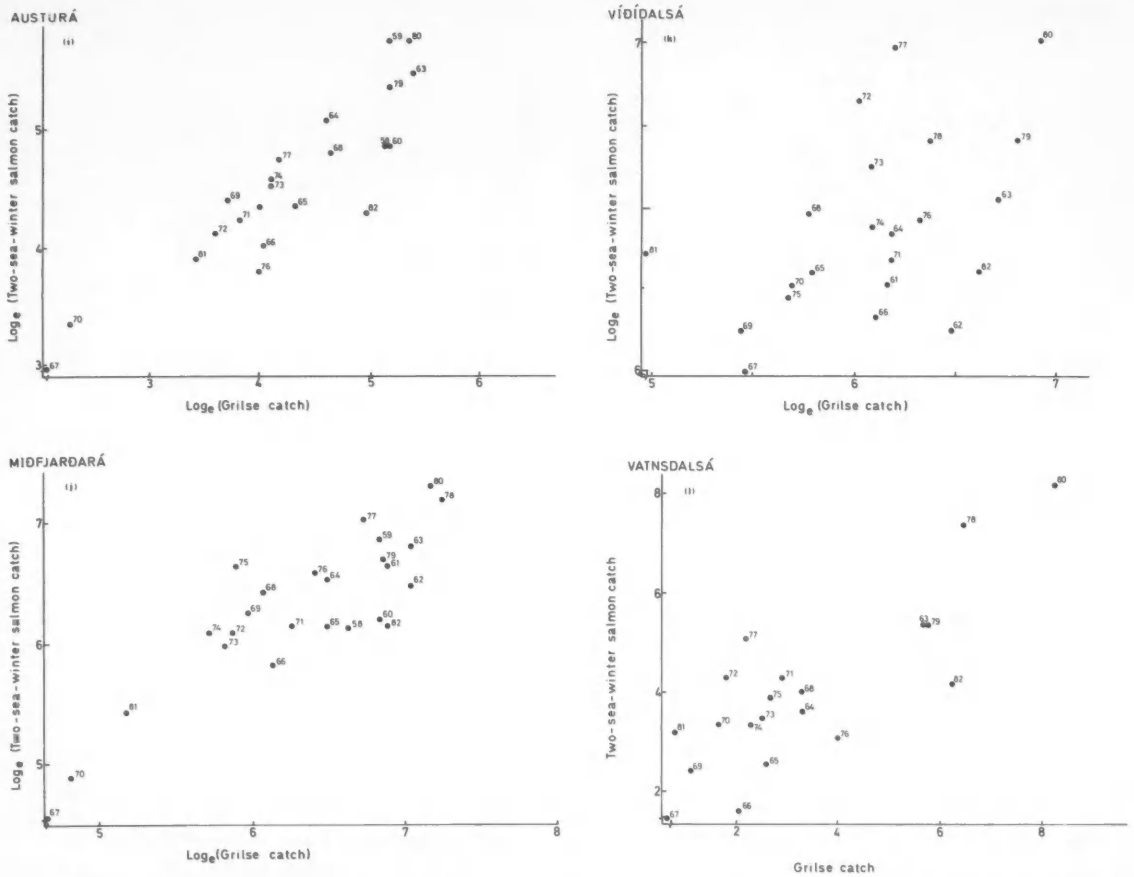

FIG. 1 (*Continued*). (i) Log catches on Austurá; log (two-sea-winter catch) = 0.679 log (grilse catch) + 1.612. (j) Log catches on Miðfjardará; log (two-sea-winter catch) = 0.785 log (grilse catch) + 1.329. (k) Log catches on Vídidalsá; log (two-sea-winter catch) = 0.288 log (grilse catch) + 4.671. (l) Catches on Vatnsdalsá (hundreds); two-sea-winter catch = 0.636(grilse catch) + 185.518.

TABLE 2. Results of tests of homoscedasticity for predictive regressions for 15 Icelandic rivers (*$p < 0.05$; **$p < 0.01$).

	Homoscedasticity test			
	Untransformed		Log-transformed	
River	τ	P	τ	P
Laxá í Kjós	0.01	0.93	−0.13	0.38
Laxá í Leirársveit	0.36	0.02*	0.19	0.23
Laxá í Dölum	0.42	<0.01**	0.31	0.01**
Fáskrúd	0.18	0.15	0.01	0.96
Langadalsá	0.25	0.13	−0.22	0.20
Hrútafjardará	0.43	0.01**	0.11	0.53
Vesturá	0.15	0.28	−0.15	0.28
Núpsá	0.13	0.35	0.03	0.82
Austurá	0.50	<0.01**	0.34	0.02*
Midfjardará	0.29	<0.05*	0.03	0.85
Vídidalsá	0.11	0.46	0.04	0.78
Vatnsdalsá	0.07	0.65	−0.09	0.56
Laxá á Ásum	0.34	0.03*	−0.03	0.85
Vesturdalsá	0.19	0.20	−0.51	<0.01**
Hofsá	0.17	0.27	−0.22	0.15

wider range of regression points. Vídidalsá, which had the most variable grilse to salmon ratio, yielded many large, older salmon that may have been misclassified by weight–frequency curves. For example, fish classified as three-sea-winter may be large two-sea-winter males. More scales are needed to verify and improve age determination for Icelandic rivers, especially for rivers such as Vídidalsá with large, older fish. Improved age determination will lead to better separation of weight frequency curves and more accurate predictions.

For several rivers (e.g. Midfjardará, Laxá í Leirársveit, Fáskrúd, and Laxá í Kjós), omission of the 1975 data point would have considerably improved the correlation coefficients. That several rivers should independently show low ratios of grilse to salmon for this smolt class indicates that consistent, widespread environmental influences act on the grilse to salmon ratios. Scarnecchia (1983) documented the correlation between sea temperatures (and accompanying air and river temperatures) and variations in percentages of grilse and older salmon *between* different Icelandic stocks of Atlantic salmon. Such factors must also produce variations in grilse to salmon ratios *within* a river. Another possible reason for anomalous 1975 data points is that yield to escapement (Y/E) ratios for grilse in 1974 may have been abnormally low, or the Y/E ratio for two-sea-winter

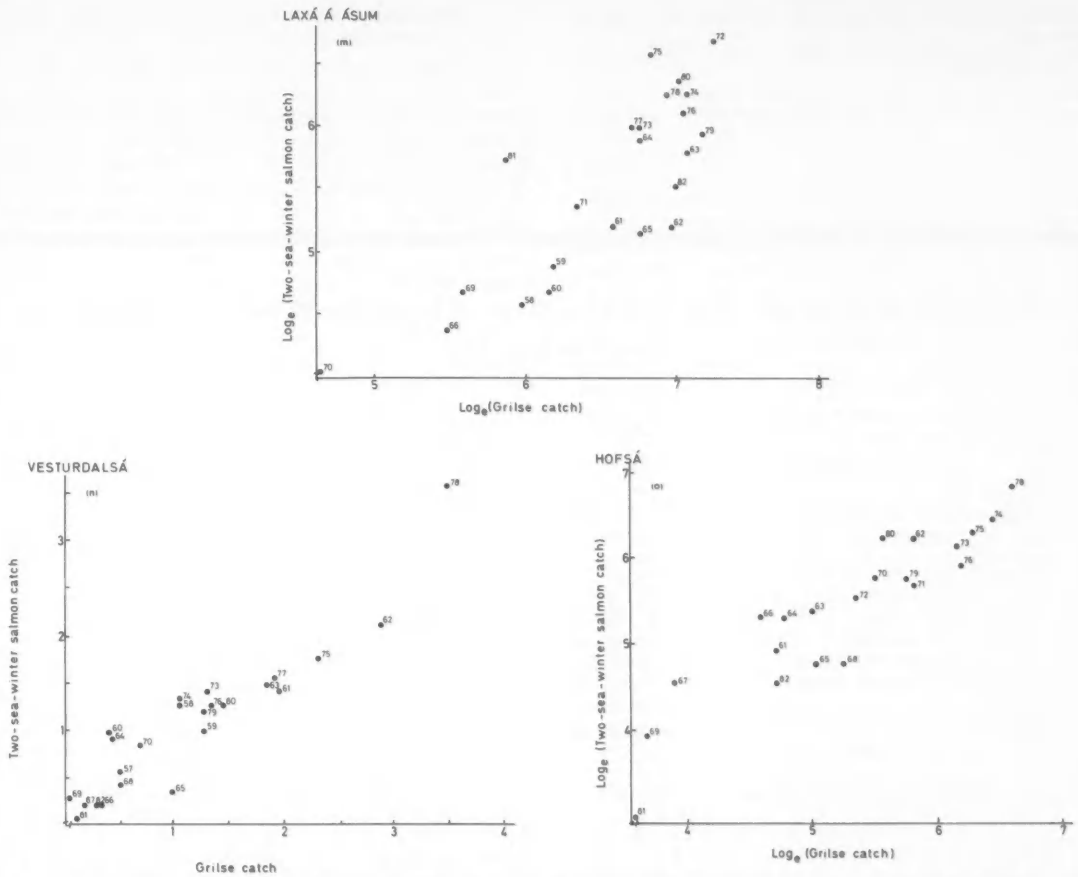

FIG. 1 (*Concluded*). (m) Log catches on Laxá á Ásum; log (two-sea-winter catch) = 0.919 log (grilse catch) − 0.476. (n) Catches on Vesturdalsá (hundreds); two-sea-winter catch = 0.796(grilse catch) + 11.522. (o) Log catches on Hofsá; log (two-sea-winter catch) = 0.928 log (grilse catch) + 0.487.

salmon in 1975 may have been unusually high. Escapement data are needed to better understand how Y/E ratios vary with such factors as relative strength of successive smolt classes, weather during the angling season, and streamflows. Effects of long-term fluctuations in ratios of grilse to two-sea-winter salmon can be partly compensated for by using predictive equations based on catch data over fewer consecutive years, or for both short-term and long-term influences, residuals can be related to prospective influential environmental variables or age-selective fishing.

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Growth Rates of Five Freshwater Algae in Well-Buffered Acidic Media

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Growth rates for five freshwater algae, *Asterionella formosa*, *Stephanodiscus hantzschii*, *Scenedesmus* sp., *Cryptomonas ozolini*, and *Anabaena flos-aquae*, in media ranging in pH from 5.0 to 7.5 using three zwitterionic buffers, MES, PIPES, and TES, were determined. These buffers supported similar growth rates when compared with each other in treatment groups of similar pH. For pH values below 6.0 no growth occurred or growth rates were significantly reduced in some treatment groups for all species except *Cryptomonas*. In some cases, these lowered growth rates were partially or completely restored by reducing trace metals in the media by one or two orders of magnitude. We suggest that these buffers could provide a useful technique for investigating the physiological responses of phytoplankton in lakes undergoing acidification.

Les auteurs ont déterminé les taux de croissance de cinq algues dulçaquicoles, soit *Asterionella formosa*, *Stephanodiscus hantzschii*, *Scenedesmus* sp., *Cryptomonas ozolini* et *Anabaena flos-aquae*, dans des médiums au pH variant de 5,0 à 7,5 et additionnés des trois solutions tampons hermaphrodites MES, PIPES et TES. Ces trois solutions tampons entraînaient des taux de croissance semblables chez les groupes traités, pourvus d'un pH semblable. Quand le pH était inférieur à 6,0, aucune croissance ne se produisait ou les taux de croissance étaient significativement réduits dans certains groupes traités de toutes les espèces sauf *Cryptomonas*. Parfois, ces taux de croissance amoindris étaient partiellement ou complètement rétablis par la diminution, de l'ordre d'un ou deux degrés des oligo-métaux dans les médiums. Les auteurs suggèrent que ces solutions tampons pourraient représenter une technique utile pour l'étude des réactions physiologiques du phytoplancton dans les lacs en voie d'acidification.

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The response of aquatic organisms to acidification has received growing interest in recent years. In particular, phytoplankton distributions in acid lakes have shown some distinct patterns. Dinoflagellates, cryptomonads, and some chlorophyte algae generally seem to predominate in acidic habitats, whereas most blue-green algae and diatoms are usually absent at pH values below approximately 4–5 (Brock 1973a, 1973b; Kwiatkowski and Roff 1976; Almer et al. 1978). The diatoms are probably the most widely studied algal group with respect to pH (Lowe 1974), especially because they are indicators of past environmental conditions (Nygaard 1956; Meriläinen 1967; Del Prete and Schofield 1981). A recent study by D. Charles (Dep. Biol., Indiana Univ., Bloomington, IN 47405, unpubl. data) shows that planktonic diatoms are entirely eliminated below pH 5.8 in Adirondack lakes affected by acid precipitation.

Because pH is the master variable for almost any biochemical reaction, it can influence algal growth and distributions in various ways. One possibility is the effect pH has on the inorganic carbon system that controls the chemical form of the carbon sources for autotrophic algae (for reviews, see Goldman et al. 1972; Talling 1976). Ambient pH determines which carbon form predominates, and research has centered on the differential use of CO_2 or HCO_3^- as carbon sources by different algae (Raven 1970; Shapiro 1973; Moss 1973). This may explain why, for example, *Scenedesmus* (which can use HCO_3^-) is generally found in more neutral habitats, whereas *Chlorella* (which only uses CO_2) is restricted to slightly more acidic conditions (Raven 1970; Goldman et al. 1972). Because pH may change the form and availability of trace metals, it has been proposed that ambient pH levels could strongly influence trace metal toxicity or limitation (Moss 1973; Droop 1974). That the concentrations of free ions, not total metal concentrations, control their toxicity or limitation for algal growth has

recently been well established (Sunda and Guillard 1976; Huntsman and Sunda 1980; Petersen 1982; Brand et al. 1983).

Our objective was to report and explain the growth rates of five planktonic algae (two diatoms, one green, one cryptomonad, and one blue-green) in well-buffered media of pH values from 5.0 to 7.5. Zwitterionic buffers were used to maintain media pH throughout each experiment. This approach is preferable to simply setting the pH at inoculation (Moss 1973). To test the hypothesis that trace metals (i.e. zinc, copper, etc.) become more available and thus more toxic under acidic conditions, we also determined algal growth rates in acidic media (5.0–6.0) where metal concentrations had been reduced to counteract this possible pH-induced toxicity.

Materials and Methods

The two diatoms used, *Asterionella formosa* Hass., and *Stephanodiscus hantzschii* Grun., were isolated by E. van Donk from lake Maarsseveen, The Netherlands; *Scenedesmus* sp. was isolated by S. S. Kilham from Lake Michigan, U.S.A.; *Cryptomonas ozolini* Sküja (UTEX – LB2194) was isolated by R. Stemberger and D. Fuller from Douglas Lake, Michigan; and *Anabaena flos-aquae* (Lyng.) Breb. was of unknown origin. Cultures were grown in 25 × 150 mm Pyrex tubes with 25 mL of a modified WC medium (Guillard 1975). Cultures were incubated in a constant environment chamber at 20°C, lighted with cool white fluorescent bulbs, which provided 200 $\mu E \cdot m^{-2} \cdot s^{-1}$ on a 14 h light : 10 h dark cycle.

The basic WC medium used in all treatments was modified by adding boron (400 μmol $B \cdot L^{-1}$) and by reducing the copper and zinc levels to 10% of the normal levels in WC. To this was added one of three zwitterionic buffers chosen for excellent buffering capacity, low metal ion binding constants, and low biochemical interference with the algal cells (Good et al. 1966; Ferguson et al. 1980). The buffers used were 2-(*N*-morpholino)ethanesulfonic acid (MES, pKa = 6.15), piperazine-*N*,*N*′-bis(2-ethanesulfonic acid (PIPES, pKa = 6.82), and *N*-tris-(hydroxymethyl)methylaminoethanesulfonic acid (TES, pKa = 7.5). We added 400 $mg \cdot L^{-1}$ of each buffer (2.05 mmol $MES \cdot L^{-1}$, 1.17 mmol $PIPES \cdot L^{-1}$, 1.75 mmol $TES \cdot L^{-1}$) to the modified WC, which was then adjusted to the proper pH with NaOH before autoclaving. Six treatment groups were also set up with MES (pH 5.0, 5.5, 6.0) using 1:10 and 1:100 dilutions of the modified trace metal mix. After autoclaving and regassing, media pH values were rechecked; they showed little variation (a maximum of 0.10 pH units) from values set before sterilization.

Growth rates were measured by in vivo fluorometry using a Turner Designs model 10 fluorometer according to a technique described by Brand et al. (1981). Fluorometric measurements were taken daily for each culture over a period of 6–8 d (before logarithmic growth ceased) after which an aliquot from each culture was transferred to fresh media. The growth rate for each 6- to 8-d replicate was then calculated by least-squares regression over the straightest points (fit by eye over at least 3-d of growth) using $\log_{10}$ transformed fluorescence measurements plotted against days, and recorded as per day. Correlation coefficients for all regressions were never less than $r = 0.96$. Cell counts over 3 d were also made with a Sedgwick–Rafter cell to check the accuracy of growth measurement by fluorescence. Regressions of fluorescence versus cell numbers always had correlation coefficients of at least $r = 0.95$. Five replicates were run for each treatment group, with means and standard deviations being calculated for each group. Occasionally, cultures required one replication before they became acclimated to the media, and these significantly lower initial data points were eliminated from final calculations. Treatment group growth rates were then compared with control growth rates using one-way ANOVA or Student's *t*-test (where appropriate) at a significance level of 0.05.

Results

Average growth rates for all treatment groups are shown in Table 1. In general, significantly reduced growth rates were observed only in groups with pH values below 6.0. Species' growth rates in the reduced metal groups showed either no effect (*Cryptomonas*) or were significantly higher than their simple MES counterparts at the same pH (*Anabaena* at 5.0, 5.5; *Asterionella* at 5.0; *Stephanodiscus* at 6). Furthermore, some of these higher rates were, as with *Asterionella*, not significantly different from their control growth rates. Where two treatment groups using different buffers were set at the same pH (6.0, 7.0), growth rates were similar; thus, the buffers themselves appeared to cause no additional variation.

In only one treatment group (5.0 MES) did *Asterionella formosa* exhibit a significantly reduced growth rate ($0.50 \cdot d^{-1}$) from the control rate of $0.70 \cdot d^{-1}$. Both metal dilution groups at pH 5.0 showed higher growth rates than 5.0 MES, thus bringing *Asterionella* growth rates nearly up to the control rate.

Stephanodiscus hantzschii did not grow in any treatment group below pH 6.0, and it grew at pH 6.0 only when the modified trace metal mix was diluted to 1:10. Growth rates both for this group ($0.63 \cdot d^{-1}$) and for 6.5 PIPES ($0.80 \cdot d^{-1}$) were significantly lower than the control rate ($1.05 \cdot d^{-1}$). Growth rates approached the control rate above pH 6.5 in both PIPES and TES treatment groups.

Except for the MES group at pH 5.0, *Scenedesmus* grew at significantly reduced rates as compared with the control rate ($1.13 \cdot d^{-1}$) in all groups below pH 6.0. In no case did reducing metal concentrations restore growth rates completely to the control rate, and only at pH 5.5 did reducing metals significantly increase growth rates from the simple MES group at this pH. At pH 6.0 and above, *Scenedesmus* growth rates for all buffers were similar to the control rate.

No treatment groups for *Cryptomonas ozolini* exhibited growth rates significantly different from the control rate ($0.72 \cdot d^{-1}$) except the PIPES group at pH 6.5 ($0.45 \cdot d^{-1}$). Why this isolated group at an intermediate pH would have such a low growth rate is not known. Some *Cryptomonas* growth rates in groups below pH 6.0 appeared to be slightly reduced from the control rate, but they were not significant.

Anabaena flos-aquae exhibited no growth in simple MES media below pH 6.0, but it grew at rates quite close to control growth ($0.75 \cdot d^{-1}$) in all treatment groups at or above pH 6.0. Reduced metal concentrations improved growth at pH 5.0 ($0.24 \cdot d^{-1}$ for 1:10 and $0.30 \cdot d^{-1}$ for 1:100 dilutions) and restored growth to control levels at pH 5.5.

Discussion

Except for *Cryptomonas*, all other algae tested exhibited significantly reduced growth at some pH levels below 6.0 in modified WC media. The two diatoms tested exhibited much different tolerances to low pH values. *Asterionella* was able to grow in all treatment groups, but the centric *Stephanodiscus* did not grow below pH 6.5. Growth in the green alga *Scenedesmus* was significantly reduced below pH 6.0, and the blue-green alga *Anabaena* could not grow in the modified WC below pH 6.0.

TABLE 1. Mean growth rates (d^{-1}) for each species and treatment group (SD in parenthesis). MES 1:10 and MES 1:100 represent groups where trace metals were reduced from control levels by these amounts. Growth rates that are significantly lower than control at the 0.05 significance level are indicated with an asterisk. The control group consisted of the modified WC medium without additional buffers or metal reductions (pH 7.4). NG = no growth.

	pH						
Treatment	5.0	5.5	6.0	6.5	7.0	7.5	Control
Asterionella formosa							0.70 (0.15)
MES	*0.50 (0.04)	0.69 (0.08)	0.68 (0.15)				
MES 1:10	0.59 (0.05)	0.67 (0.08)	0.64 (0.15)				
MES 1:100	0.64 (0.07)	0.62 (0.12)	0.67 (0.15)				
PIPES			0.66 (0.09)	0.63 (0.12)	0.79 (0.07)		
TES					0.85 (0.10)	0.78 (0.13)	
Stephanodiscus hantzschii							1.05 (0.14)
MES	NG	NG	NG				
MES 1:10	NG	NG	*0.63 (0.11)				
MES 1:100	NG	NG	NG				
PIPES			NG	*0.80 (0.07)	0.99 (0.07)		
TES					1.04 (0.12)	1.01 (0.07)	
Scenedesmus sp.							1.13 (0.07)
MES	0.79 (0.26)	*0.85 (0.05)	1.14 (0.15)				
MES 1:10	*0.80 (0.10)	*0.94 (0.04)	0.85 (0.21)				
MES 1:100	*0.61 (0.15)	*0.93 (0.04)	1.02 (0.05)				
PIPES			1.06 (0.04)	1.15 (0.05)	1.14 (0.04)		
TES					1.19 (0.09)	1.17 (0.02)	
Cryptomonas ozolini							0.72 (0.12)
MES	0.64 (0.09)	0.71 (0.05)	0.74 (0.05)				
MES 1:10	0.67 (0.04)	0.64 (0.08)	0.70 (0.04)				
MES 1:100	0.72 (0.08)	0.70 (0.04)	0.67 (0.03)				
PIPES			0.66 (0.06)	*0.45 (0.07)	0.72 (0.06)		
TES					0.74 (0.05)	0.71 (0.02)	
Anabaena flos-aquae							0.75 (0.06)
MES	NG	NG	0.65 (0.06)				
MES 1:10	*0.24 (0.04)	0.71 (0.13)	0.70 (0.08)				
MES 1:100	*0.30 (0.06)	0.65 (0.05)	0.71 (0.09)				
PIPES			0.67 (0.03)	0.68 (0.03)	0.75 (0.04)		
TES					0.70 (0.07)	0.71 (0.10)	

Growth rate reductions in our more acidic treatment groups possibly result from increases in the activity of free metal ions in the more acidic media, thus inducing metal toxicity. For some species of algae tested here (*Asterionella*, *Anabaena*), reducing the metal concentrations of these media seemed to counteract this apparent acid-induced toxicity (Table 1). Very few investigators have directly approached the interaction between external pH and metal toxicity although trace metal effects are especially sensitive to control of their activity or speciation (Sunda and Guillard 1976; Huntsman and Sunda 1980; Petersen 1982; Brand et al. 1983). Thus, increased metal activities induced by increased H^+ concentrations could increase metal toxicity in algae. For diatoms, trace metals such as copper and zinc may exert their influence on silica acid uptake (Reuter and Morel 1981; Brand et al. 1983), which may explain the growth rate reductions we found in *Asterionella* and *Stephanodiscus* (Table 1). Metal uptake (and its subsequent effects) may be affected by H^+, i.e. by changing the H^+ gradient across the cell membrane necessary for copper uptake (Kanazawa and Kanazawa 1969), or by directly competing with Cu^{2+} for cell membrane uptake sites (Steemann-Nielsen and Kamp-Nielsen 1970).

Although not detectable in our results, pH-induced changes in the inorganic carbon species of the media may also cause significant changes in algal growth. Near neutrality, HCO_3^- is the dominant form of carbon, but as the pH drops, dissolved CO_2 becomes increasingly important. Moss (1973) stated that several oligotrophic species usually require CO_2 as a carbon source, thus explaining their restriction to habitats below pH 8.6. *Scenedesmus* can use HCO_3^- as a carbon source, which may explain its restriction to more neutral or basic habitats (Raven 1970; Goldman et al. 1972). Our results for *Scenedesmus* showed reduced growth in almost all treatment groups below pH 6.0 (Table 1). Similarly, blue-green algae may also use HCO_3^- as a carbon source because Shapiro (1973) found that CO_2 additions to lake enclosures (which subsequently lowered pH) resulted in a reduction of blue-green populations. We believe, however, that carbon source differences did not reduce the growth rate of *Anabaena* below pH 6.0 because we were able to restore growth at pH 5.5 and induce partial growth

at pH 5.0 by reducing metal concentrations, which had no apparent affect on the carbon source (Table 1).

Other researchers have also suggested that nutrient uptake and metabolism may be affected by pH and thus alter algal growth. Phosphate uptake is strongly affected by pH for *Ankistrodesmus* (Ullrich-Eberius and Simonis 1970) and for *Anabaena variabilis* (Healey 1973). Ullrich (1972) also considered external pH to alter interior cytoplasm pH, thus affecting internal phosphate metabolism. Furthermore, maximum ammonium uptake rates have been inversely related to increasing pH (Zevenboom 1980), and Healey (1977) reported that because pH dependence on NH_4^+ and urea uptake is species specific, it may help explain competitive interactions between some algae. However, nutrients were present in excess in the modified WC, so it is unlikely that nutrient deficiencies at low pH values reduced growth in our cultures. Furthermore, because trace metal reductions in our experiments occasionally restored growth in the more acidic treatments, we doubt that pH-induced nutrient uptake changes were of major importance.

We have shown that five species of planktonic freshwater algae from four different groups can be grown well in three zwitterionic buffers: MES, PIPES, and TES. For species that were apparently sensitive to pH levels of 5.0–6.0, reducing the trace metal levels usually restored growth rates, often back to control rates. This investigation is the first to our knowledge to quantify the extent of growth reduction of these five species under acidic conditions. We hope that the use of zwitterionic buffers will help us to understand the mechanisms involved in shifts in species composition of phytoplankton in lakes undergoing acidification.

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Effect of Diet on the Immune Response of Rainbow Trout (*Salmo gairdneri*)[1]

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Blazer, V. S., and R. E. Wolke. 1984. Effect of diet on the immune response of rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 41: 1244–1247.

To compare the effect of diet on the immune response of rainbow trout (*Salmo gairdneri*), we maintained fish on either a commercial feed or a laboratory prepared (control) diet for 12–16 wk before antigenic exposure. The immune response to two antigens, sheep red blood cells (SRBC) and *Yersinia ruckeri*, was assessed. Both T-cell (migration inhibition factor) and B-cell (plaque-forming cell) responses to SRBC were measured. The plaque-forming cell response and the humoral (serum antibody) responses to *Y. ruckeri* were assayed. In addition, the phagocytic ability of peritoneal macrophages was assessed as a nonspecific resistance factor. We found that fish maintained on the commercial diet had a significantly lower immune response when compared with fish fed the control diet, although all fish appeared healthy and suffered no mortalities throughout the experiment. We indicate the importance of considering the effects of diet on immunity and disease resistance in future feed formulations.

Afin de comparer l'incidence du régime sur l'immunoréaction de la truite arc-en-ciel (*Salmo gairdneri*), les auteurs ont nourri des individus avec des aliments commerciaux ou de la nourriture préparée en laboratoire (groupe témoin) pendant 12 à 16 sem avant l'exposition aux antigènes. Ils ont évalué l'immunoréaction à deux antigènes, soit les hématies de mouton (HM) et *Yersinia ruckeri*, et quantifié les réactions des cellules T (facteur d'inhibition de la migration) et B (cellules formatrices de plaques de lyse) aux HM. Ils ont aussi analysé les réactions des cellules B et des humeurs (anticorps du sérum) à *Y. ruckeri*. De plus, la capacité phagocytique des macrophages péritonéaux a été évaluée comme facteur de résistance non spécifique. Les auteurs ont découvert que les poissons nourris d'aliments commerciaux avaient une immunoréaction significativement inférieure par rapport aux truites maintenues au régime témoin, quoique tous les poissons semblaient en santé et qu'aucun ne soit mort au cours de l'expérience. Ils soilignent l'importance de prendre en considération les effets du régime sur l'immunité et la résistance aux maladies au cours de la préparation des aliments.

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Infectious disease is a major source of loss in intensive fish culture. Because many potential fish pathogens are ubiquitous inhabitants of the fishes' environment, major disease outbreaks often occur when the balance among fish, etiologic agent, and environment is upset (Sniesko 1973). The role of environmental stress, whether due to poor water quality, crowding, handling, or pollutants, is well established as a predisposing factor to disease (reviewed by Wedemeyer et al. 1976).

It is reasonable to assume that available levels and balance of dietary nutrients may also influence disease susceptibility. There are only a few reports of such nutritional research in the literature. Durve and Lovell (1982) showed that increased levels of ascorbic acid reduced mortalities of fingerling channel catfish (*Ictalurus punctata*) experimentally infected with *Edwardsiella tarda*. Two times the suggested level of vitamin A (30 000 I.U./kg) was reported to decrease mortalities of Atlantic salmon (*Salmo salar*) fingerlings due to *Ichthyophthirius multifiliis* (Malikova et al. 1961). Feed with high trace elements (Fe, Cu, Mn, Co, I, and F), low calcium content, or high vitamin A and C levels significantly lowered the incidence of bacterial kidney disease in Atlantic salmon. The highest incidence was observed in fish maintained on commercial feed (Paterson et al. 1981).

The quality of food is also important in disease resistance. A difference in mortalities due to bacterial kidney disease in coho salmon (*Oncorhynchus kisutch*) was observed when fish were maintained on diets with corn gluten versus cottonseed meal (Wedemeyer and Ross 1973). Taniguichi (1983) observed a difference in the disease incidence of streptococcosis between yellowtails (*Seriola quinquiradiata*) fed frozen versus thawed food.

Although the above reports show that disease incidence and diet are related, no attempt has been made to determine the basis for this relationship. Nonspecific defense mechanisms such as macrophage phagocytosis and intracellular killing, inflammation, and various nonspecific serum factors, as well as specific immunity, are important in disease resistance. The purpose of our study was to elucidate possible mechanisms for the nutritional effects on disease susceptibility.

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Materials and Methods

Rainbow trout, *Salmo gairdneri* (≈115 g), from certified disease-free stock were maintained in a 90% reuse system at the Aquaculture Center of the University of Rhode Island. They were acclimated for 6 wk and fed Rangen's trout pellets prior to beginning the feeding study. The water temperature ranged from 11 to 15°C during the 4-mo feeding period and from 15 to 19°C during the sampling period.

Two diets were compared, a commercially available feed (Rangen's 5-cm trout pellet) and a laboratory prepared diet (control) based on the Oregon test formulation (NRC 1973) wetted to 16% moisture (Table 1). This diet was prepared every 7–10 d and stored frozen to minimize nutrient loss. The commercial diet was obtained in 22.7-kg bags, which were stored frozen until opened and at 20°C while used for feed. Each experimental group consisted of 150 fish. The feeding rate was based on body weight and water temperature following Phillips (1970). To determine the feeding rate, we weighed 30 fish from each group every 3 wk. The rate ranged from 1.6 to 2.3% body wt/d (as fed basis) for the control feed and from 1.2 to 2.0% body wt/d for the commercial feed.

We measured the immune response to two separate antigens, sheep red blood cells (SRBC) and the bacterial pathogen *Yersinia ruckeri*. Fish were maintained on the experimental diets for 12 wk before exposure to SRBC and for 17 wk before exposure to *Y. ruckeri*. For exposure, fish were anesthesized with MS 222 (Tricaine methanesulfonate) at a concentration of 0.15 mg/mL water. Each fish was injected intraperitoneally with either 0.2 mL of a 10% suspension of washed SRBC in phosphate-buffered saline, pH 7.2 (PBS), or 0.2 mL of a suspension containing 2 mg formalin-killed, washed *Y. ruckeri*/mL PBS.

TABLE 1. Composition of diets fed to rainbow trout.

Control diet		Commercial diet proximate analysis	
Ingredients[a]	% dry wt	Ingredients	Amount
Casein (vitamin free)	49.50	Crude protein (min.)	38.0%
Dextrin	15.60	Crude fat (min.)	8.0%
Vitamin premix[b]	2.00	Crude fiber (max.)	4.0%
Mineral premix[c]	4.00		
Gelatin	8.70	Ascorbic acid[e]	0.088%
Cod liver oil	7.50	α-Tocopherol[f]	20 I.U./kg
Corn oil	2.50		
Choline chloride	0.50		
Ascorbic acid	0.12		
α-Tocopherol[d]	0.16		
α-Cellulose	9.42		

[a]All ingredients were obtained from United States Biochemical Organization.

[b]Composition (% in premix): thiamine (0.32), riboflavin (0.72), niacinamide (2.56), biotin (0.008), calcium pantothenate (1.44), pyridoxine (0.24), folic acid (0.096), menadione (0.08), vitamin A, 250 000 I.U./g (0.5), vitamin B_{12}, 3000 μg/g cobalamine (0.2667), *i*-inositol (12.5), ρ-aminobenzoic acid (2.0), and α-cellulose (79.0793).

[c]Composition (% in premix): $CaCO_3$ (2.1), $CaHPO_4 \cdot 2H_2O$ (73.5), citric acid (0.205), $2CuC_6H_5O_7 \cdot 5H_2O$ (0.046), $FeC_6H_5O_7 \cdot 5H_2O$ (0.558), MgO (2.5), $Mn_3(C_6H_5O_7)_2$ (0.835), KI (0.001), K_2HPO_4 (8.1), K_2SO_4 (6.8), NaCl (3.06), Na_2HPO_4 (2.14), $Zn_3(C_6H_5O_7 \cdot 2H_2O)$ (0.133), NaF (0.002), and $CoCl_2$ (0.02).

[d]α-Tocopherol content of 250 I.U./g.

[e]Analyzed by the 2,6-dichloroindophenol method (AOAC 1970).

[f]Analyzed by Winston Laboratories, Inc., Ridgefield Park, NJ, using high-pressure liquid chromatography.

The immune function assays and sampling schedule are described by Blazer et al. (1984) and Blazer and Wolke (1984). Each assay was run at the time of peak response as determined in preliminary experiments. Briefly, the immune response to SRBC was measured using the migration inhibition factor (MIF) assay, 2 d postinoculation, and the plaque-forming cell (PFC) assay, 15 d postinoculation. We evaluated the immune response to *Y. ruckeri* with the passive PFC assay, 14 d after injection, and serum agglutination, 30 d after injection. For the passive PFC assay, SRBC were labelled with O-antigen of *Y. ruckeri*. Head kidney cell suspensions were used for both the PFC and MIF assays. We used the phagocytic index of peritoneal macrophages as an indicator of nonspecific resistance. Macrophages were collected from the peritoneal cavities of fish maintained on the experimental diets for 16 wk. Adherent macrophages were allowed to phagocytize 0.91-μm latex beads for 30 min at room temperature. Slides were then rinsed, fixed, and stained. One hundred macrophages on each slide were scored for the number of beads per macrophage.

At the conclusion of the experiment, tissue samples of 10 fish from each group were fixed in 10% neutral buffered formalin and routinely prepared for histopathological examination. We examined the following tissues: liver, spleen, head and hind kidney, thymus, anterior and posterior intestine, stomach, gills, skeletal muscle, and skin.

The commercial feed was analyzed for ascorbic acid content using the 2,6-dichloroindophenol method (AOAC 1970). Winston Laboratories, Inc., Ridgefield Park, NJ, determined the α-tocopherol content using high-pressure liquid chromatography.

Statistical significance was tested using Student's *t*-test. Agglutination titers were transformed by $\log_{(x)}$ to correct for nonnormality.

Results

All fish continued to grow and appeared healthy throughout the experiment. There were no mortalities and no lesions observable by light microscopy in either group. There was a significant difference in growth rate. Fish fed the commercial diet were an average weight of 253 g at 12 wk and 312 g at 17 wk, while those fed the control diet weighed 196 g at 12 wk and 204 g at 17 wk. The diets were of entirely different composition (Table 1) and probably differed in caloric value and digestibility although these were not determined. The commercial diet contained 88 mg ascorbic acid/kg and 20 I.U. α-tocopherol/kg.

Despite the enhanced growth rate, the immune response of fish maintained on the commercial feed was significantly lower than that of control fish (Table 2). Both MIF (T-cell function test) and PFC (B-cell function test) responses to SRBC were significantly decreased ($p < 0.05$) in fish fed the commercial diet. For fish responding to *Y. ruckeri*, the humoral response as measured by serum antibody titers was significantly higher in control fish (mean reciprocal titer 432; range 128–2048) compared with fish fed the commercial feed (mean 172; range 64–512). Although the PFC response to *Y. ruckeri* was lower in fish fed the commercial diet (47 PFC/10^6 lymphocytes), it was not significantly different from control fish (69 PFC/10^6 lymphocytes).

TABLE 2. Differences in immune response of rainbow trout with a commercial and laboratory diet. Values are mean ± 1 SE (*N*). Numbers followed by an asterisk are significantly lower than controls at $p \leq 0.05$.

Immune function assay	Treatment	
	Commercial diet	Control diet
Sheep red blood cell injected		
% migration inhibition	25.3±4.8* (8)	67.8±5.1 (8)
PFC/10^6 lymphocytes	22±4* (10)	180±48 (10)
Y. ruckeri injected		
PFC/10^6 lymphocytes	47±9 (12)	69±7 (11)
Agglutination titers	172±9* (12)	432±10 (12)
Nonspecific factors		
Phagocytic index	11±0.5* (8)	21±0.7 (8)

The phagocytic ability of peritoneal macrophages was also affected by diet. Macrophages from fish maintained on the commercial feed phagocytized significantly fewer beads (11 beads/macrophage) than macrophages from control fish (21 beads/macrophage).

Discussion

We hypothesized that commercial feeds may not contain levels of certain nutrients to allow for optimal disease resistance and functioning of the immune system. Diet, although not adversely affecting the fish by either gross or histologic examination, did influence the immune response and macrophage function. Fish maintained on a control diet had an enhanced cellular and humoral response as well as increased phagocytic ability of peritoneal macrophages when compared with fish fed a commercial feed.

The battery of tests used elucidated some mechanisms for dietary influences on disease susceptibility. MIF and PFC responses are routinely used in homeotherms as T- and B-cell function assays, respectively. Definitive evidence that salmonids have both morphologically and functionally distinct populations of lymphocytes has not yet been demonstrated. However, they are capable of responses associated with both T- and B-cells in other animals. Recently, using monoclonal antibodies, it has been shown that separate lymphocyte subpopulations can be distinguished in fish based on differences in cell surface and/or cytoplasmic determinants (Lobb and Clem 1982; Secombes et al. 1983).

Because the two diets used were of totally different composition, identification of the factor(s) responsible for the enhanced immune response of the control fish is impossible. A number of vitamins and minerals have been found to affect immunity in homeotherms (Gross and Newberne 1980). Two possible nutrients for the immune enhancement in our study are ascorbic acid and vitamin E. The levels of both nutrients in the control diet were well above the minimum daily requirement (NRC 1973). Also, the preparation and storage of the control diet was such that nutrient loss would be at a minimum. Because ascorbic acid is extremely labile it is easily destroyed in the processing and storage of commercial fish feed (Slinger et al. 1979).

Durve and Lovell (1982) found a correlation between dietary ascorbic acid levels and mortalities of channel catfish experimentally infected with *E. tarda*. No mechanism for the increased resistance was reported. However, it has since been shown that dietary ascorbic acid level does affect nonspecific resistance factors. Rainbow trout fed a diet with 120 mg ascorbic acid/kg feed (dry wt) had a significantly decreased total serum iron-binding capacity and phagocytic index of peritoneal macrophages when compared with fish maintained on a diet containing 1200 mg/kg feed (Blazer 1982).

Vitamin E has also been found to be important in the immune response of fish. Rainbow trout fed a diet low in α-tocopherol had a significantly reduced immune response even though they appeared healthy and showed no signs of a vitamin E deficiency. Cellular and humoral immunity, as well as macrophage function, was impaired in these fish (Blazer and Wolke 1984).

These results indicate that assessing the immune response and other defense mechanisms provides a means of evaluating subtle effects of diet that are extremely important in disease resistance. Possibly, the currently accepted requirements for certain nutrients are not adequate on the basis of disease resistance. If so, it would be advantageous to feed increased levels of these nutrients before and during stressful periods, i.e. at times disease outbreaks are most likely to occur. Further research is necessary to identify nutrients capable of enhancing disease resistance and also to determine the levels necessary for this enhancement.

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An In Situ Substratum Fertilization Technique: Diatom Colonization on Nutrient-Enriched, Sand Substrata

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Using an in situ substratum enrichment method, we assessed the effects of nutrient release from sand substrata on the community structure of attached diatoms in a sand-bottomed, northern Michigan stream. Sand from the stream bottom was washed, sterilized, and then consolidated into small plastic petri dishes with agar solutions enriched with various concentrations of $NaNO_3$ and KH_2PO_4. Laboratory estimates of nutrient release rates were performed over a 144-h period with uncolonized substrata having different agar and nutrient concentrations. Release rates decreased 10-fold in an exponential fashion with no significant differences between replicates. Agar concentrations had no significant effect on release rates, although the rates were proportional to nutrient concentrations in the substratum. Racks of substrata were installed parallel to the stream current flow and retrieved after a 6-wk colonization period. Using multiple comparisons of treatment means for both nutrients and algal taxa, we found no differences between control and NO_3 enrichments; significant differences were found, however, between PO_4 and $NO_3 + PO_4$ (N:P = 25:1) treatment means relative to each other and the control. Diatom biovolume was two times as great on PO_4 treatments and four times greater on $NO_3 + PO_4$ treatments. Effects of PO_4 and NO_3 enrichment appear to be taxa specific, with PO_4 and $NO_3 + PO_4$ treatments favoring *Navicula* and *Nitzschia* spp. Control and NO_3 treatments were dominated by *Cocconeis placentula* Ehr. and *Achnanthes minutissima* Kutz.

En utilisant une méthode in situ d'enrichissement du substrat, les auteurs ont évalué l'incidence de la mobilisation des bioéléments du substrat sablonneux sur la structure de la communauté de diatomées fixées dans un cours d'eau à fond sablonneux du nord du Michigan. Le sable prélevé du fond a été lavé, stérilisé et mélangé dans de petits plats de pétri avec des solutions d'agar enrichies de diverses concentrations de $NaNO_3$ et de KH_2PO_4. En laboratoire, on a quantifié pendant 144 h les taux de mobilisation des bioéléments de substrats non colonisés contenant différentes concentrations de bioéléments et d'agar. Les taux de mobilisation ont baissé par un facteur de 10 de façon exponentielle, sans différences significatives entre les doubles. Les concentrations d'agar n'avaient aucune incidence significative sur les taux de mobilisation quoique les taux étaient proportionnels aux concentrations de bioéléments dans le substrat. Des grilles de substrat ont été installées parallèles au courant et récupérées après une période de colonisation de 6 sem. En utilisant des comparaisons multiples des moyennes de traitement obtenues pour les bioéléments et les diverses espèces d'algues, les auteurs n'ont découvert aucune différence entre le groupe témoin et le substrat enrichi de NO_3 ; par contre, ils en ont trouvé entre les moyennes des groupes enrichis de PO_4 et de $NO_3 + PO_4$ (N:P = 25:1) et entre ces groupes et le témoin. Le volume de diatomées était deux fois et quatre fois plus élevé en présence de PO_4 et de $NO_3 + PO_4$ respectivement. L'incidence du PO_4 et du NO_3 semble être spécifique ; ainsi, l'addition de PO_4 et de $NO_3 + PO_4$ semble favoriser *Navicula* et *Nitzschia* spp. *Cocconeis placentula* Ehr. et *Achnanthes minutissima* Kutz. peuplaient principalement les traitements témoins et les traitements au NO_3.

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In terrestrial ecosystems, the spatial distribution of many plant species has been closely correlated with the spatial distribution of soil nutrients (Pigott and Taylor 1964; Hanawalt and Whittaker 1976; Tilman 1982). Although the gross contribution of nutrients from marine and lake sediments to the primary production of overlying waters has received wide attention (Golterman et al. 1969; Fitzgerald 1970; Entsch et al. 1983), little has been published about the relationship between substratum fertility and species composition of attached periphyton. Observations that certain periphyton taxa reach high numbers on potentially nutrient-rich substrata have led several investigators to postulate a nutritional relationship between substratum and attached diatom communities (Cholnoky 1968; Linkins 1973; Lee et al. 1975). C. M. Pringle (University of Michigan, Ann Arbor, MI, unpubl. masters thesis, 1979) observed dense mats of *Navicula tripunctata* (O. Mull.) Borey and *Nitzschia linearis* (W. Sm.) covering larval chironomid tubes, similarly suggesting that a nutritional benefit was being derived by diatoms from the metabolic activities of the larval occupants.

Periphytic taxa locating themselves in nutrient-rich microenvironments have an adaptive advantage (Hellebust and Lewin 1977) that is especially significant in stream systems where spatially dependent nutrient reutilization is important (Ball and Hooper 1963; Short and Maslin 1977). If nutrients can be directly taken up by periphyton before becoming diluted in the water column and transported downstream, such tight coupling would represent a lower spatial limit within the framework of "nutrient spiralling" (Webster 1975; Newbold et al. 1981; Elwood et al. 1981a, 1981b).

Experimental field studies relating stream periphyton species composition and biomass to nutrient enrichment have been confined to direct nutrient additions to flowing water by whole-stream enrichment (Huntsman 1948; Warren et al. 1964; Elwood et al. 1981b) or through utilization of flow-through systems (Stockner and Shortreed 1978; Peterson et al. 1983). The substratum fertilization technique we describe here is introduced as a new in situ method to manipulate periphyton communities experimentally. To evaluate this technique we first examined NO_3 and PO_4 release rates from sand–agar substrata and the effects of agar concentration on release rates. Field studies then assessed effects of NO_3 and PO_4 singly and in combination on diatom biovolume and community composition in a northern Michigan stream.

Materials and Methods

Field portions of this study were conducted in Carp Creek, a second- to third-order stream located entirely on The University of Michigan Biological Station tract, Cheboygan County, MI. This sand-bottomed stream is spring-fed, exhibiting a constant discharge and relatively stable temperatures (10 ± 3°C in July). The stream is alkaline and nutrient poor, with nutrient levels during the study period averaging 4 $\mu g\ PO_4 \cdot L^{-1}$, 35 $\mu g\ NO_2 + NO_3N \cdot L^{-1}$, and 33 $\mu g\ NH_3N \cdot L^{-1}$. Carp Creek flows ~2.6 km to Burt Lake through an undisturbed wooded area composed mainly of conifers (*Thuja occidentalis*, *Pinus strobus*, and *Tsuga canadensis*).

Sand collected from the streambed was washed and autoclaved to kill attached microorganisms and then consolidated into plastic disposable petri dishes (5.2 cm diameter, 1.2 cm deep), with agar solutions enriched with various concentrations of $NaNO_3$ and KH_2PO_4. Each dish contained ~40 g of sand and 10 mL of agar solution. Agar and sand were thoroughly mixed and compacted such that liquid agar filled all interstitial spaces between sand grains. After solidification, the substratum was scraped flush with the lip of the petri dish, creating a hard, flat surface for periphyton colonization.

A laboratory experiment, in a three-level hierarchical design, was performed to characterize substratum nutrient release rates and to evaluate general effects of agar, NO_3, and PO_4 concentrations on rates of release. Twelve wide-mouth 4-L glass jars were acid rinsed, filled with 3 L of distilled water, and then placed in an incubator–shaker (Psychrotherm, New Brunswick) at 10°C. Artificial substrata placed within incubated jars were made with three different agar concentrations: 2.0, 2.5, and 3.0%. Within each of these treatments there were two different combinations of NO_3 and PO_4 concentrations (0.5 mol $NO_3 \cdot L^{-1}$:0.5 mol $PO_4 \cdot L^{-1}$ and 1.5 mol $NO_3 \cdot L^{-1}$:1.5 $PO_4 \cdot L^{-1}$), with two replicates per combination. Mixing of the water column above the substratum was achieved through the shaking action of the platform within the incubator. At time intervals of 0, 4, 8, 12, 24, 36, 49, 60, 72, 97, 120, and 144 h, the water in each jar was also vigorously stirred, after which a 20-mL water sample was removed with an acid-cleaned beaker. Samples were frozen and stored in acid-cleaned polyurethane bottles and analyzed for PO_4 and NO_3 using a Technicon II autoanalyzer (APHA 1975). Soluble reactive phosphate and nitrate were measured utilizing the molybdenum blue technique and the cadmium reduction technique, respectively.

In substratum construction for field experiments, 2.0% agar solutions were utilized. Agar solutions in three sets of plates were respectively enriched with 0.5 mol $NaNO_3 \cdot L^{-1}$, 0.5 mol $KH_2PO_4 \cdot L^{-1}$, and 0.5 mol $NaNO_3 \cdot L^{-1}$ + 0.02 mol $KH_2PO_4 \cdot L^{-1}$ (N:P = 25:1). A fourth set of control plates contained pure agar with no nutrients. Treatments consisted of three replicate substrata that were glued to pine boards (6.0 × 60.0 cm) and anchored with wire to the sand streambed of Carp Creek in an open sunny site during June–July of 1982 (Fig. 1). To minimize the variability of physical factors affecting substrata, we placed boards in a median range of current velocities (28–34 $cm \cdot s^{-1}$) and depths (10–15 cm below the water surface), such that the surfaces of the sand–agar plates were parallel with the current flow. Current velocities were measured with a standard Pygmy Gurley meter.

Previous studies in Carp Creek (C. M. Pringle, unpubl. data) indicated that periphyton biovolume reaches an asymptote after a colonization period of about 6 wk. Coring of our artificial sand–agar substrata has shown that diatoms are not located in sediment below the upper 3 mm of substratum during the day. Because of these observations, substrata were retrieved from the stream after a 6-wk colonization interval, and the top 3 mm of agar and sand was carefully cut out with a razor blade. This layer was placed in a 50-mL beaker and diluted with 25 mL of distilled water. The sample was then mixed for 10 min with a magnetic stirrer and decanted into a 100-mL beaker. The remaining sand grains were rinsed with 25 mL of fresh distilled water and the suspension again decanted into the 100-mL beaker. This procedure resulted in almost complete periphyton separation from sand grains, as evidenced by microscopic scanning of residual grains. Samples (0.4 mL) were then filtered (0.22-μm Millipore® filter) and subsequently cleared with immersion oil to allow algal cell enumeration under a compound microscope (1000×).

Diatoms comprised >90% of the periphyton biovolume on all treatments and counts were restricted to diatom taxa. At least 500 diatom frustules per slide were counted. The cell volume

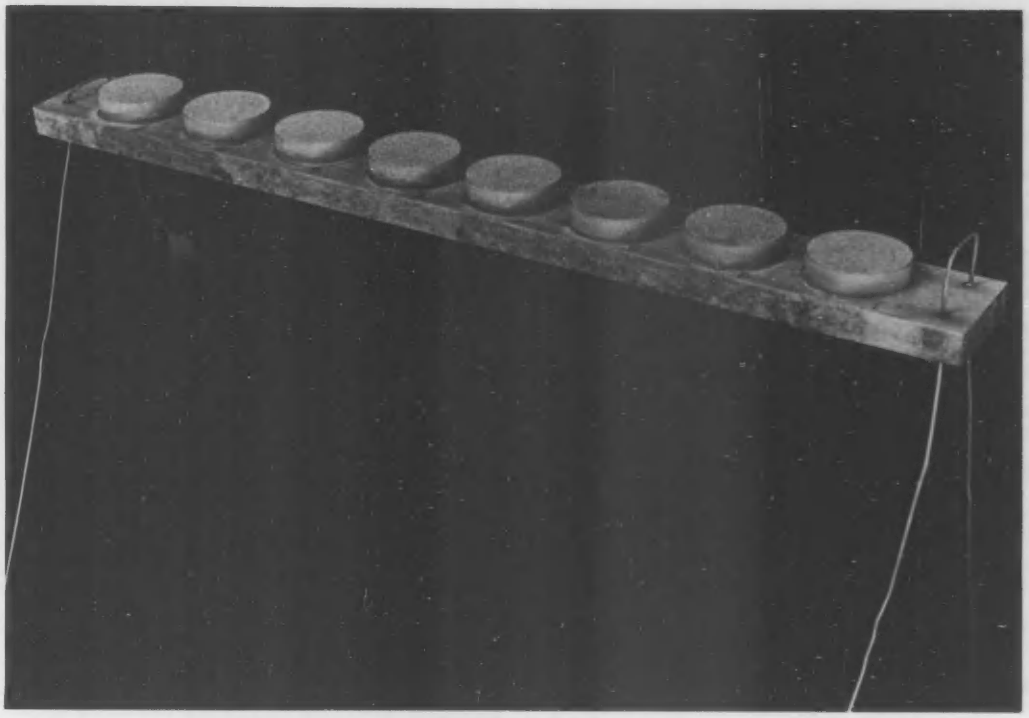

FIG. 1. Enriched sand–agar substrata consolidated into plastic petri dishes and mounted on a pine board.

of specific taxa was estimated by entering mean diatom measurements into geometric equations that best describe the three-dimensional shape of the frustule. Diatom cells were measured with an ocular micrometer and substage adjustment to determine length, width, and height. A minimum of 25 cells per diatom taxon has proven adequate in determining biovolumes (C. M. Pringle, unpubl. data).

Results

The laboratory nutrient release experiment indicated that release rates of NO_3 and PO_4 decreased exponentially through time. A 3 × 2 factorial ANOVA (three levels of agar, two levels of NO_3 and PO_4, two replicates per cell), based on the mean release rates through the 144-h time interval, indicated that agar concentrations of 2.0, 2.5, and 3.0% did not significantly affect NO_3 and PO_4 release rates ($P < 0.01$). However, those substrata having the 1.5 mol $NO_3 \cdot L^{-1}$ + 1.5 mol $PO_4 \cdot L^{-1}$ concentrations had release rates significantly higher than plates with the 0.5 mol $\cdot L^{-1}$ concentrations of these same nutrients ($P < 0.01$). NO_3 and PO_4 release rates representative of this experiment and those agar and nutrient concentrations used for the field experiments are illustrated in Fig. 2. N:P ratios of release rate were not significantly correlated ($r = -0.12$, $P < 0.01$) at N and P concentrations used, suggesting that N:P ratios during release either remain constant or vary in a random fashion.

Diatom analysis of substratum plates after a 6-wk colonization period in Carp Creek indicated that the NO_3 + PO_4 treatment (N:P = 25:1) supported almost four times the biovolume (57.43×10^7 $\mu m^3 \cdot cm^{-2}$) found on control substrata (14.68×10^7 $\mu m^3 \cdot cm^{-2}$; Fig. 3). The 0.5 mol $PO_4 \cdot L^{-1}$ treatment supported a biovolume only two times greater (28.92×10^7 $\mu m^3 \cdot cm^{-2}$) than the control whereas the 0.5 mol $NO_3 \cdot L^{-1}$ treatment alone supported only a slightly higher biovolume.

To assess results of pilot field studies, we used two-way ANOVA, and both treatment effects and the interaction term were highly significant ($P < 0.001$). Multiple comparisons (Student–Newman–Keuls test, $P = 0.05$) of treatment biovolume means for both nutrients and algal taxa indicated no difference between the control and NO_3 enrichments. However, the PO_4 and NO_3 + PO_4 additions were significantly different from each other and the first two treatments (control and 0.5 mol $NO_3 \cdot L^{-1}$).

The control and NO_3 treatments were dominated by *Cocconeis placentula* Ehr. and *Achnanthes minutissima* Kutz., whereas the PO_4 and NO_3 + PO_4 treatments were characterized by a predominance of motile pennate diatoms (e.g. *Navicula* and *Nitzschia* spp.; Fig. 3). Taxa biovolume means fell into three different groups: (1) *A. minutissima* and *C. placentula*, (2) *Navicula* spp., and (3) *Nitzschia* spp. and the "other" category. The significant interaction term indicates that enrichment with PO_4 alone and NO_3 + PO_4 produced taxa-specific effects. Addition of PO_4 triggered a fourfold increase in *Navicula* and a threefold increase in *Nitzschia* whereas *A. minutissima* and *C. placentula* biovolumes were not significantly different from the control. The NO_3 + PO_4 treatment resulted in a greater than 10-fold increase in *Navicula* and *Nitzschia*, with *A. minutissima* and *C. placentula* displaying significantly lower biovolumes relative to the control.

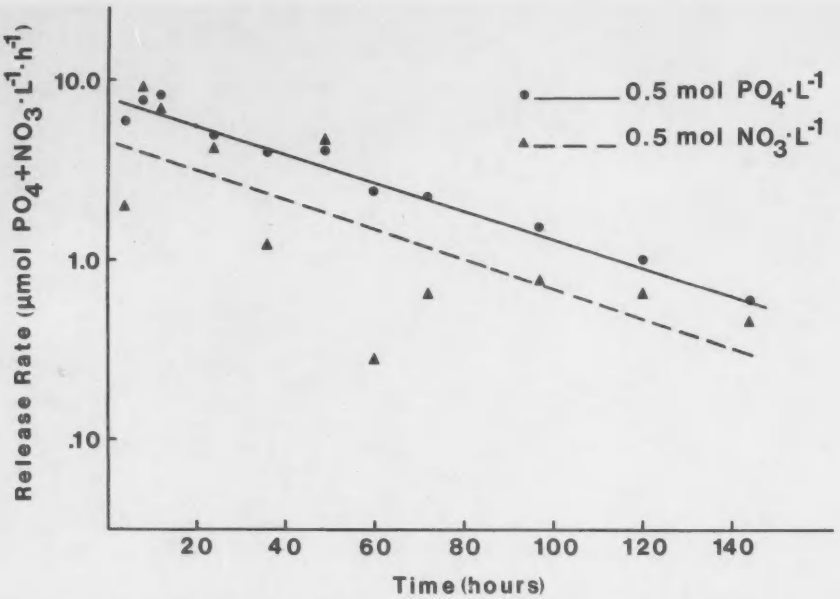

FIG. 2. Mean phosphate (PR) and nitrate (NR) release rates from enriched, 2.0% agar substrata into distilled water at 10°C. Linear regressions of release rates versus time on a semi-logarithmic scale indicated an exponential rate decrease. For PO_4, ln PR = $-0.02T + 2.09$ where $r^2 = 0.97$, $s_b = 0.01$, and $n = 11$. For NO_3, ln NR = $-0.02T + 1.48$ where $r^2 = 0.58$, $s_b = 0.01$, and $n = 11$.

Discussion

Our technique detected taxa-specific effects that were similar to previously observed distribution patterns on potentially nutrient-rich natural substrata in Carp Creek (C. M. Pringle, unpubl. data). *Navicula* and *Nitzschia* spp. dominated the diatom assemblages covering clumps of decomposing mayfly (*Baetis vagans*) exuviae and the larval retreats of the chironomid *Pseudodiamesa* cf. *pertinax* (Garrett) in Carp Creek. The tubes of *P. pertinax* are composed of consolidated sand grains and support high diatom biovolumes (112.9×10^7 µm^3·cm^{-2}). *Achnanthes minutissima* and *C. placentula* were the dominant diatom taxa on wood substrata unmodified by chironomid tubes and were likewise predominant on unenriched control and NO_3 treatments.

Alteration of N:P ratios also resulted in differences in species composition that were proportionally similar to results obtained in nutrient enrichment studies of other oligotrophic streams (Stockner and Shortreed 1978; Peterson et al. 1983). In these studies, increases in NO_3 alone had no appreciable effects on algal growth. Likewise, preliminary results from Carp Creek indicate no significant differences between diatom biovolume on control and NO_3 treatments. Additions of NO_3 + PO_4 (N:P = 25:1) resulted in almost four times the biovolume of the control whereas addition of PO_4 alone resulted in a twofold increase. Similarly, Stockner and Shortreed (1978) found that trebling concentrations of both NO_3 and PO_4 (N:P = 35–40:1), over ambient concentrations, resulted in greatest algal growth. They likewise observed that when PO_4 alone was trebled, thereby reducing the N:P ratio to 10–13:1, maximum growth was only a little greater than half that seen when both N and P were trebled. Peterson et al. (1983) found that PO_4 addition alone and PO_4 + NH_4NO_3-N enrichment resulted in significantly higher levels of chlorophyll *a* and CO_2 uptake (from six to eight times that of control).

In contrast with previous studies in which nutrients were added at a constant rate into flowing water, release rates from our artificial substrata decrease exponentially through time. This pattern of exponential decay is similar to nutrient release rate curves observed for naturally decomposing substrata such as leaves (Hynes and Kaushik 1969; Howarth and Fisher 1976; Elwood et al. 1981b). In the laboratory, release rate curves reached an asymptote within 6 d, with an estimated 78.5% P and 82.3% N left in substrata. Greater diatom biovolume observed on nutrient-enriched substrata after a 42-d colonization period indicated significant long-term effects of in situ enrichment.

The method we describe here displays reproducible results and its compact design facilitates implementation in the field. Also, it more realistically reproduces the texture of natural substrata as compared with artificially barren substrata such as glass slides. This latter, widely used substratum has been found to select against filamentous and loosely attached metaphytonic species with a higher stature than tightly adhering forms (Brown 1976). Since release rates from artificial sand–agar substrata were found to be independent of agar concentration, physical manipulation of the substratum is possible. Agar concentrations can be manipulated to affect the firmness of the substratum surface and hence its resistance to biogenic influences such as burrowing by chironomid larvae. Artificial substrata can also be enriched with a variety of substances, and substance-specific release rates ascertained. This may allow distinctions to be made between periphyton community response along a resource ratio gradient to specific elements within the gross array of materials that are found in and often added to natural systems.

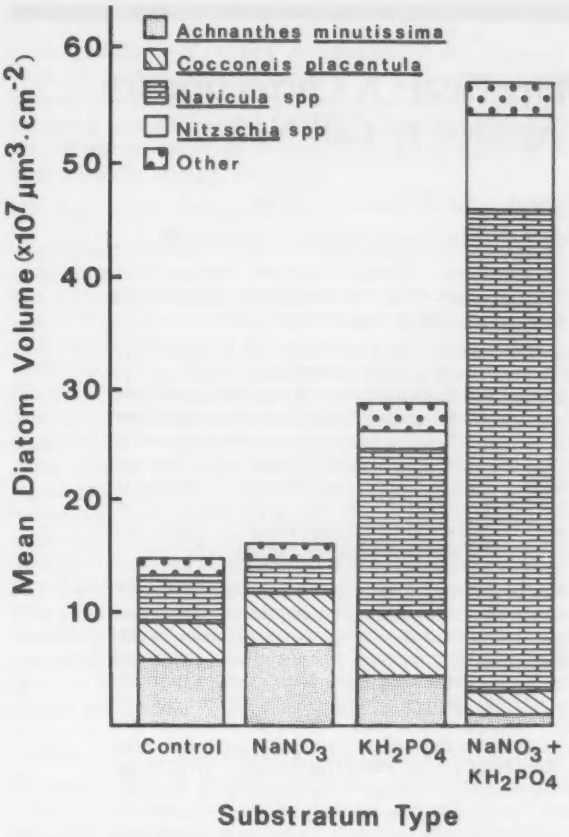

FIG. 3. Relative biovolume abundance of diatoms colonizing sand–agar substrata in Carp Creek. $NaNO_3$ substratum type = 0.5 mol $NaNO_3 \cdot L^{-1}$, KH_2PO_4 substratum type = 0.5 mol $KH_2PO_4 \cdot L^{-1}$, and $NaNO_3$ + KH_2PO_4 substratum type = 0.5 mol $NaNO_3 \cdot L^{-1}$ + 0.02 mol $KH_2PO_4 \cdot L^{-1}$ (N:P = 25:1).

For example, many vitamins, amino acids, and other organic materials influence the growth and metabolism of periphyton, but species and community effects have yet to be elucidated. Lastly, when used in conjunction with methods of direct fertilization of the water column (Stockner and Shortreed 1978; Peterson et al. 1983), this substratum enrichment technique will enable closer examination of the relative contributions of nutrients from substrata and the water column to periphyton community structure.

Acknowledgments

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Size Selectivity of Passive Fishing Gear: A Correction for Encounter Probability Applied to Gill Nets

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Rudstam, L. G., J. J. Magnuson, and W. M. Tonn. 1984. Size selectivity of passive fishing gear: a correction for encounter probability applied to gill nets. Can. J. Fish. Aquat. Sci. 41: 1252–1255.

The probability of catching a fish in a gill net may be separated into two components: (1) the probability of the fish encountering the net and (2) the probability of the fish being caught and retained in the net. We consider the probability of encounter to be directly proportional to the distance travelled by the fish during the sampling period. This distance will increase with fish size if different-sized fish swim for the same amount of time because swimming speed increases with fish size. Routine swimming speed measured in the laboratory for three size-classes of bloater (*Coregonus hoyi*) increased with length to the 0.8 power. Corrections for encounter probability were incorporated in gill net selectivity calculations for samples of cisco (*Coregonus artedii*), a species closely related to bloater. These corrections can significantly increase the proportional estimates of smaller relative to larger animals in the estimated population structure. The approach should also be applicable to other passive fishing gear, such as longlines and set nets.

La probabilité de capture d'un poisson dans un filet maillant peut être divisée en deux composantes, soit (1) la probabilité que le poisson rencontre le filet et (2) la probabilité que le poisson soit capturé et retenu dans le filet. Les auteurs considèrent que la probabilité de rencontre est directement proportionnelle à la distance parcourue par le poisson pendant la période d'échantillonnage. Cette distance s'accroît en fonction de la taille du poisson si des individus de différentes longueurs nagent pendant la même période car la vitesse de nage augmente par rapport à la taille. Les vitesses de nage mesurées systématiquement en laboratoire chez le cisco de fumage (*Coregonus hoyi*) appartenant à trois classes de longueur ont augmenté en fonction de la longueur à la puissance 0,8. Des corrections pour la probabilité de rencontre ont été incorporées dans les calculs de la sélectivité des filets maillants pour les échantillons de cisco de lac (*Coregonus artedii*), espèce étroitement apparentée au cisco de fumage. Ces corrections peuvent nettement accroître les estimations proportionnelles des petits animaux par rapport aux gros dans la structure estimée de la population. Cette approche devrait aussi être applicable à d'autres engins de pêche comme la palangre et le filet mouillé.

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Size selectivity of gill nets (the probability of capturing a certain size of fish in one unit of operation of the gear) is best considered as a characteristic of the entire fishing operation (Lagler 1968; Hamley 1975). Therefore, gear selectivity will depend both on the probability that a fish encounters the net and on the probability that the fish is caught and retained by the net (Regier 1975; Hamley 1975). Factors that affect either of these probabilities will affect net selectivity.

In a comprehensive review of gill net selectivity, Hamley (1975) described methods used to date to construct selectivity curves (plots of the selectivity of a net as a function of some measure of fish size) from the size distribution of catches in different mesh sizes. The shape of these curves, at least for species that are caught primarily by wedging, e.g. coregonines, is similar with different mesh sizes when selectivity is plotted against the ratio of fish girth to mesh perimeter (McCombie and Fry 1960; McCombie and Berst 1969). A combined selectivity curve for a set of nets differing in mesh size can be obtained by summing the selectivity curves of each net. This requires that the relationship between the efficiencies of different nets towards the fish size that they catch the best is known. This maximum efficiency is often assumed to be the same for all nets used, an assumption that has been criticized (Ricker 1949; Regier and Robson 1966; Hamley 1975). With walleyes (*Stizostedion vitreum vitreum*), Hamley and Regier (1973) found that nets with larger mesh were more efficient than those with smaller mesh.

At least part of this greater efficiency of larger mesh nets results because larger fish have a higher probability of encountering a net than do smaller fish (Lagler 1968). In this paper we describe how an expression for length-dependent encounter probability can be incorporated into selectivity calculations, and we illustrate the potential magnitude of bias our method can correct for, using gill net catch data on cisco (*Coregonus artedii*). Encounter probability is considered to be directly proportional to distance travelled by a fish during the sampling period. We posit that distance travelled is proportional to speed of spontaneous swimming activity (routine speed) (see Magnuson 1978).

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Selectivity Calculations

The probability of catching an individual of size l by a net of mesh size m may be separated into two independent probabilities: (1) the probability that the fish will encounter the net during a sampling period, $P(E_l)$, and (2) the probability that the fish will be caught and retained by the net of mesh size m after encounter, $P(R_{lm})$. Therefore:

$$(1) \quad C_{lm} = P(E_l) \cdot P(R_{lm}) \cdot N_l$$

where C_{lm} = the number of fish of size l caught and retained per sampling period in a net of mesh size m and N_l = the number of fish of size l occurring in the lake.

The expression for $P(R_{lm})$ was obtained by fitting a function to Berst's (1961) selectivity curve for cisco from Lake Huron (Table 1). This curve was derived using the method of McCombie and Fry (1960). In the terminology of Regier and Robson (1966), Berst combined type B selectivity curves (i.e. graphs of selectivity versus mesh size for a given fish size) plotted against fish girth : mesh perimeter ratios into a single type B master curve by adjusting each curve to a unit area. This master curve also represents a type A curve (i.e. a graph of selectivity versus fish size for a given mesh size) because the ratio girth : perimeter is a function of both fish size and mesh size (Hamley 1975). The assumption that each type B curve has the same area is equivalent to considering $P(E_l)$ as a constant. Therefore, Berst's selectivity curve is proportional to the probability that the fish is caught and retained after encounter ($P(R_{lm})$). Since girth can be related to fish length, $P(R_{lm})$ can be written as a function of fish length and mesh perimeter (Table 1).

When $P(E_l)$ is considered to be a function of fish size, as in this paper, each type B curve should be scaled according to the value of $P(E_l)$ for the fish length in question. From these curves, new type A curves can be constructed. Our combined function $(P(E_l) \cdot P(R_{lm}))$ represents such type A curves, since, for each fish length l, the value of $P(R_{lm})$ is scaled by $P(E_l)$. For the sake of clarity, we keep the two functions separate.

The encounter probability should be directly proportional to the distance travelled by the fish during the sampling period. This distance is directly proportional to routine speed if (1) different-sized fish swim for the same amount of time during the sampling period and (2) different-sized fish occupy the same habitat. The degree to which these conditions are satisfied will depend on the fish species studied. Since swimming speed can be approximated as a power function of fish length (Bainbridge 1958; Yates 1983), we obtain

$$(2) \quad P(E_l) = A_1 \cdot l^z$$

where A_1 is a constant.

The exponent in the expression for routine and/or sustained swimming has been determined for several fishes and is often about 0.5 (e.g. see Magnuson 1970; Brett and Glass 1973; Wu and Yates 1978). Since routine speeds of coregonines have not been reported, we measured this parameter for bloater, *Coregonus hoyi*, a cisco from the Laurentian Great Lakes. The fish were kept in large aquaria, 1.5 and 2.5 m in diameter, at the Center for Great Lakes Studies, University of Wisconsin-Milwaukee. Bloater and cisco are in the same subgenus (Scott and Crossman 1973) and behave similarly in captivity (F. Binkowski, Center for Great Lakes Studies, University of Wisconsin-Milwaukee, pers. comm.). Both species swim continuously, day and night, in one direction around the tank. Routine swimming speeds were measured for three size-classes of bloaters held in separate aquaria. The individuals were timed as they swam around the tank past two points 30 cm apart. All measurements were made between 8 and 10 a.m. on June 20, 1983. The temperature in all three tanks was between 12.3 and 12.5°C. The value for the length exponent calculated from these measurements, 0.8, was used for cisco (Table 2).

Inserting expressions for $P(R_{lm})$ from Table 1 and $P(E_l)$ from equation 2 into equation 1, we obtain

$$(3) \quad C_{lm} = (A_2 \cdot f(l, m)) \cdot (A_1 \cdot l^{0.8}) \cdot N_l$$

where A_1 and A_2 are constants.

Given our assumptions, the expression $(A_2 \cdot f(l, m)) \cdot (A_1 \cdot l^{0.8})$ is the absolute selectivity coefficient of a net with mesh size m towards fish of size l. To obtain N_l the values for the constants are needed. In most instances these constants are not known and only relative values for the numbers of fish in each length group can be obtained. By scaling this selectivity coefficient to 1 for a particular size fish (in our example, a 20-cm-long cisco), we obtain a curve of the relative selectivity coefficient as a function of fish length. The relative selectivity curves for each mesh size can be summed to yield a total selectivity curve for a set of nets (Fig. 1). A corrected size distribution is obtained by dividing the catch for each length group by its relative selectivity coefficient.

TABLE 1. Equations used for calculating retention probability for cisco. The equations were obtained by fitting a modified logistic function (Thornton and Lessem 1978) to the increasing and decreasing parts of the selectivity curve presented by Berst (1961) for Lake Huron cisco using the method of least squares. The equation for fish girth was also derived from Berst (1961) by a linear approximation of his two equations.

Equations

$$P(R_{lm}) = A_2 \cdot f(l, m)$$

$$f(l, m) = z/(l + z)$$

where $z = 1.10 \cdot 10^{-8} \cdot e^{17.4x}$ for $x < 1.26$ and

$z = 2.81 \cdot 10^{8} \cdot e^{-13.1x}$ for $x > 1.26$

$$x = ((0.399 \cdot l) + 12.7)/2m$$

Symbols

$f(l, m)$: retention function dependent on fish length and mesh size
x: girth/mesh perimeter
m: mesh size (strech mesh, mm), half of the perimeter
l: fish length (total length, mm)

Example

Field methods — Samples were from Big Muskellunge and Sparkling lakes (Vilas Co., Wisconsin) in August 1981 and

TABLE 2. Laboratory measurements of routine swimming speed of three size-classes of bloater in relation to their length. Linear regression: ln (swimming speed) = 0.6 + 0.8 ln (length), $r^2 = 0.650$, standard error of exponent = 0.05.

	Total length of fish			Routine swimming speed		
Age-class	Mean (cm)	SD	*N*	Mean (cm/s)	SD	*N*
I+	10.8	0.6	10	12.6	2.7	50
II+	15.3	0.6	10	18.6	4.3	50
IV–VI+	24.9	3.1	32	25.0	3.5	50

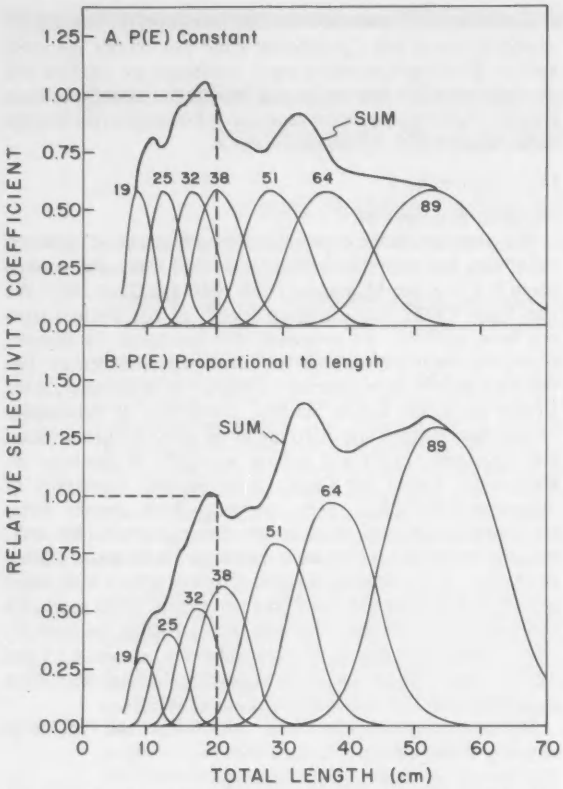

FIG. 1. Relative selectivity curves for cisco assuming that their probability $P(E)$ of encountering the net is (A) constant and (B) proportional to fish length to the 0.8 power. The selectivity curves for individual nets (mesh sizes 19, 25, 32, 38, 51, 64, and 89 mm stretch mesh) and for the whole set of nets are presented. The selectivity coefficients for the whole set of nets are scaled to 1 for 20-cm-long fish. Uncorrected selectivity curves and girth–length relationships were derived from Berst (1961) (see Table 1).

from Lake Mendota (Dane Co., Wisconsin) in September 1982 (Rudstam 1983). In 1981, cisco populations were sampled with six vertical gill nets, each with a different mesh size (19, 32, 38, 51, 64, and 89 mm stretch mesh). In 1982, a 25-mm mesh net was added. All nets were 4 m wide and 18 m deep and were suspended from surface to bottom along the 18-m depth contour.

Calculations — We calculated uncorrected catch per unit effort (CPUE) and percent age structure and then corrected for retention probability and retention probability plus encounter probability for the three populations of cisco (Tables 3 and 4).

Incorporating the correction for encounter probability illustrates the possible magnitude of bias associated with uncorrected estimates of abundance. For example, the CPUE in Lake Mendota is 46% of the CPUE in Sparkling Lake before and 21% after corrections for encounter probabilities were included (Table 3). This occurs because the fish in Mendota were larger than those in Sparkling; thus, more fish per unit time would have encountered the net relative to fish in Sparkling Lake. For comparisons between years within a single lake, the effect could be of similar magnitude if the size structure of the population changes with time.

TABLE 3. Catch per unit effort of cisco of all ages in three Wisconsin lakes summed from six vertical gill nets over 48 h. The catch in the 25-mm net added for Lake Mendota is not included. Catch per unit effort was calculated from (1) field data, (2) field data corrected for retention probability, and (3) field data corrected for both retention and encounter probabilities.

	Catch per unit effort (no. per set)		
Lake	(1)	(2)	(3)
Big Muskellunge	186	308	498
Sparkling	116	177	291
Mendota	65	82	60

TABLE 4. Age structure and mean length of cisco in three Wisconsin lakes sampled with vertical gill nets. Relative age structure was calculated from (1) field data, (2) field data corrected for retention probability, and (3) field data corrected for both retention and encounter probabilities.

			Age structure (%)		
Lake and year (no. caught)	Age group	Total length (cm)	(1)	(2)	(3)
Big Muskellunge,	YOY	10	64.9	78.0	86.0
1981	I+	19	31.9	19.5	12.7
(186 fish)	II+	24	2.6	2.0	1.1
	≥III+	28	0.5	0.4	0.2
Sparkling,	YOY	10	63.5	73.7	84.7
1981	I+	20	30.4	20.5	12.7
(116 fish)	II+	26	3.5	3.7	1.8
	≥III+	34	2.6	2.0	0.8
Mendota,	YOY	13	13.8	14.2	27.4
1982	I+	27	3.1	3.4	3.5
(77 fish)	V+	36	83.1	82.4	69.2

The potential magnitude of bias on age structures is also illustrated (Table 4). YOY fish made up a larger percentage of the population after corrections for encounter probability, while older fish made up a smaller percentage after the correction. In some cases the changes were large. For example, in Lake Mendota, YOY fish made up 14% of the population before and 27% after the correction, thus doubling their estimated contribution to the population.

Discussion

During a sampling period, fish of different sizes should travel a distance proportional to their swimming speed, if they have the same daily activity pattern. If fish of different sizes also occupy the same habitat, the encounter probability should be directly proportional to the swimming speed of the fish. Pelagic planktivores, such as cisco, may fulfill these conditions reasonably well. Cisco and other coregonines swim constantly in captivity (F. Binkowski, pers. comm.) and the cisco has been described as one of the most active of fishes in Wisconsin (Cahn 1927). Furthermore, all sizes appear to be distributed across the entire lake at night when almost all cisco are caught in gill nets (Engel and Magnuson 1976; Rudstam 1983). Although direct observations of the routine speed of different sized cisco in the

field were not available, our laboratory measurements on bloaters provide the best available approximation for cisco. Thus, the correction for encounter probability seems reasonable. In general, our approach should be most appropriate for schooling fishes that spend all or almost all of their time swimming, such as coregonines, scombrids, and carangids.

The effect of incorporating our size-dependent expression for encounter probability will increase with the size range of fish caught and with the size of the exponent z (equation 2). In our cisco example, the differences in encounter probability estimated by our model appear large enough to significantly bias estimates of catch per unit effort and age structure. Thus, catch curve data and mortality estimates would be biased as well. This could be an important consideration in calculation of population dynamics for a number of important fisheries that rely on passive fishing gear. Examples are tuna longline fisheries, high-sea salmon gillnet fisheries, and drift gill nets for herring. The magnitude of the correction would be directly proportional to the swimming speeds of the sizes or species of fish being compared. The correction thus could be large. For example, 75-cm-long skipjack tuna (*Katsuwonus pelamis*) have routine speeds twice that of yellowfin (*Thunnus albacares*) (Magnuson 1973) and, thus, at equal densities, they should encounter passive gear twice as often as yellowfin. For other continuously swimming species, the exponent relating speed to length may be different from the 0.8 we observed for bloater. It is 0.5 for wavyback skipjack (*Euthynus affinis*) (Magnuson 1970), 0.42–0.50 for sockeye salmon (*Oncorhynchus nerka*) (Brett and Glass 1973; Ware 1978), and 0.6 for jack mackerel (*Trachurus symetricus*) (Hunter 1971).

To investigate whether corrections for encounter probability might apply to passive fishing gear other than gill nets and fish other than cisco, we calculated the exponent in the expression for $P(E_l)$ for perch (*Perca flavescens*) caught in fyke nets and central mudminnows (*Umbra limi*) caught in minnow traps from data obtained as part of a study on density compensation (Tonn 1983). For these gear, we assume $P(R_{lm})$ to be constant for the sizes of fish normally caught. Single mesh sizes (5 mm square mesh for fyke nets and 6 mm for minnow traps) were used for each type of gear. Data were available on population size (determined through mark–recapture), catch per unit effort, and mean length of fishes for several sampling periods from June to October 1980–82 in three small bog lakes in northern Wisconsin. A log–log linear regression of (CPUE/population size) against mean length of fish resulted in an exponent of 1.6 (95% C.I. = 0.5–2.6, $N = 22$) for yellow perch and 2.7 (95% C.I. = 1.2–4.2, $N = 17$) for central mudminnows. Although these data are from three different lakes and from different time periods, they indicate an increase in efficiency of these gears towards larger fish. We attribute this increase partly to increased swimming speeds of larger fish.

A correction for encounter probability based on swimming speed may not completely account for the increased efficiency observed for larger fish after corrected for mesh size selection in gill nets. Hamley and Regier (1973) observed larger increases in selectivity of large mesh nets for walleye than could be accounted for by our corrections. Other factors may be involved, such as differences in daily activity patterns and/or habitat utilization of different size walleyes, or decreased visibility of larger mesh nets.

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PERSPECTIVES

Ecological Effects of Acid Deposition Upon Peatlands: A Neglected Field in "Acid-Rain" Research

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Gorham, E., S. E. Bayley, and D. W. Schindler. 1984. Ecological effects of acid deposition upon peatlands: a neglected field in "acid-rain" research. Can. J. Fish. Aquat. Sci. 41: 1256–1268.

Certain types of peatlands are probably highly susceptible to anthropogenic acidification, yet very little research is being done on the vulnerability of bogs and fens to acid deposition. We have documented the need for such research and for studies of the role of acidification — natural and anthropogenic — in determining nutrient availability, metal mobilization, and biogeochemical cycling by fauna and microflora. Possible effects of hydrological changes, and of drainage from acid peatlands to lakes and streams, are noted. We provide an outline of possible responses of plants and animals to acidification; these should be investigated at species, community, and ecosystem levels. Studies of peatlands as possible sources of the gaseous precursors of acid deposition are needed. Different approaches to examining the responses of peatlands to acid deposition include geographical surveys, experimental studies, short-term, long-term, and paleoecological investigations, and analysis of biogeochemical mass-balances. Finally, we emphasize the need for inclusive studies of peatlands in relation to surrounding uplands and to the streams and lakes that receive their drainage.

Quoique certains types de tourbières soient probablement très sensibles à l'acidification anthropique, peu de recherches couvrent la vulnérabilité des marais et des tourbières immergées au dépôt d'acides. Les auteurs documentent le besoin de telles recherches et d'études sur le rôle de l'acidification, soit naturelle ou anthropique, quant à la disponibilité des bioéléments, la mobilisation des métaux et le cyclage biogéochimique par la faune et la microflore. Ils notent aussi les effets possibles de modifications hydrologiques et de l'écoulement des eaux des tourbières acides dans les lacs et rivières. Ils décrivent les réactions potentielles des plantes et des animaux à l'acidification, réactions qui devraient être étudiées aux niveaux de l'espèce, de la communauté et de l'écosystème. Des études devraient porter sur les tourbières comme source possible de précurseurs gazeux de dépôts acidiques. L'examen des réactions des tourbières aux dépôts acidiques comprend les différentes approches suivantes : levés géographiques, études expérimentales, recherches à court et à long terme, recherches paléoécologiques et analyse de l'équilibre des masses biogéochimiques. Enfin, ils soulignent le besoin d'études exhaustives des tourbières par rapport aux hautes terres environnantes et aux lacs et cours d'eau qui reçoivent les eaux d'écoulement.

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Peatlands are a large and vital component of the biosphere and are believed to play a significant role in the global cycles and geochemical balances of carbon, nitrogen, and sulphur. Widespread disruption of these ecosystems by acid deposition (commonly described as acid rain) could have serious and large-scale consequences for freshwater lakes and streams. The total area of peatlands is estimated to be 420–450 million ha (Kivinen and Pakarinen 1981), including approximately 150 million ha in Canada, 150 million ha in the USSR, and 60 million ha in the United States. The amount of carbon in the global peat reservoir is estimated at approximately 150×10^{15} g, with annual carbon accumulation of about 0.2×10^{15} g (Bramryd 1981). With an average carbon content of about 50% (cf. Walmsley 1977), and a heat of combustion of about 21 $kJ \cdot g^{-1}$ (Clymo 1983), the potential energy reserve of the world's peat deposits is thus approximately 6.3×10^{18} kJ.

Peatlands and their margins are breeding grounds for a great variety of fish, furbearing mammals, and both migratory and nonmigratory birds. Many peatlands bear forests of economic value. They supply water to important lake and river systems,

provide some degree of flood control, inhibit erosion, and filter pollutants from associated streams and lakes. They also have recreational and educational value. Wetland values are discussed by Goodwin and Niering (1974) and by Greeson et al. (1979). Unfortunately, the ecology of peatlands is poorly understood and has received much less attention than that of terrestrial or aquatic ecosystems (Gorham 1982). Summaries of past and present knowledge are available in Gorham (1953a, 1957), Moore and Bellamy (1974), Radforth and Brawner (1977), Good et al. (1978), Heal and Perkins (1978), and Gore (1983).

The following definitions may be useful:

Wetland: any poorly drained area whose substrate is at least periodically saturated with or covered by water.

Peatland: a wetland ecosystem depositing more than 30 cm of peat, a substrate with a high organic content (usually 85–90% dry weight on average, and often more than 95% in bogs).

Muskeg: a northern peatland, usually with an abundance of *Sphagnum* moss, tussocky sedges, and an open growth of scrubby trees.

Bog: a peatland whose surface receives only atmospheric precipitation; it is described, therefore, as ombrotrophic. Bogs are often dominated by mosses of the genus *Sphagnum*, especially in high latitudes.

Fen: a peatland whose surface receives water that has percolated through mineral soil; it is described as minerotrophic.

Swamp: a forested wetland.

A glossary of the many special terms used in peatland science is given by Stanek (1977).

Some U.S. government agencies at both the federal and the state level have been concerned with peatland preservtion for wildlife, while other government agencies are promoting their drainage for agriculture or construction (Goodwin and Niering 1974). Canadian government agencies have been more concerned with peatland utilization, although the Muskeg Subcommittee of the Associate Committee on Geotechnical Research of the National Research Council of Canada has promoted some fundamental research in addition to its research efforts concerned with utilization and capacity to carry vehicular traffic (Radforth and Brawner 1977). No government agency in either country has, so far as we know, a clear mandate for the inclusion of peatland studies in its programs for research on acid deposition or the long-range transport of air pollutants, although at least two Canadian government agencies and one in the United States have sponsored preliminary investigations.

Many peatlands may be highly vulnerable to rapid acidification, because they have little bicarbonate buffering. Of particular concern are certain types of fen (e.g. *Carex* sedge meadows with and without *Sphagnum* moss carpets), whose surface waters have very low alkalinities (< 40 μmol·L^{-1} by old-style titration to an endpoint of pH 4.5) and pH values of about 6.0, and whose peats are almost wholly organic with very little input of silt (cf. Gorham 1967). Although such peatlands are minerotrophic, the mineral supply from soil is small and the bicarbonate so supplied is very limited. As in lakes (Glass and Loucks 1980), even small inputs of strong acids are likely to cause major declines of pH and other chemical changes with possible adverse consequences for organisms. Both humic substances and aluminum species contribute to buffering at pH values below 5, but their capacity to resist the acidification process in peatlands has not been measured. In lakes, aluminum has a buffer capacity of 111 μeq·mg Al^{-1}; humic substances have a capacity of only 7.5 μeq·mg organic carbon^{-1} but predominate in their effect because the ratio of organic carbon to aluminum is 20–200:1 (Johannessen 1980). In this connection, the filter-passing organic carbon in surface bog waters from Manitoba to Newfoundland ranges from 10 to 62 mg·L^{-1} (Gorham et al. 1984). Southeastern waters draining peatlands range up to 47 mg·L^{-1} (Alberts and Giesy 1983). Data on aluminum are very scarce; Sparling (1967) gave a range of 0.1–3.2 mg·L^{-1} in British and Irish bog waters.

It is important to recognize that acidification can occur rather suddenly once minerotrophic inputs either cease, owing to peat accumulation above the normal groundwater level, or are overwhelmed by anthropogenic acid deposition. Figure 1, which shows the relationship of pH to alkalinity in three British peatlands, mimics a titration curve in which pH drops sharply once alkalinity is exhausted. None of the 25 sites examined occupies the transition zone between pH 6 and 5, the range of minimal bicarbonate buffering. Similarly, surface waters collected from the different plant communities of the vast peatlands in northern Minnesota exhibit two distinct groupings of site pH (Fig. 2a), with a bog mode at pH 4, a fen mode at pH 6, and relatively few sites in the intermediate range of pH 5.0–5.4, although intermediate sites have probably been over-sampled in proportion to their abundance. Northern Swedish peatlands show a similar picture (Fig. 2b), as do lakes in Norway (Wright and Henriksen 1977) and Nova Scotia (Underwood et al. 1982).

A major research program should be initiated to study the

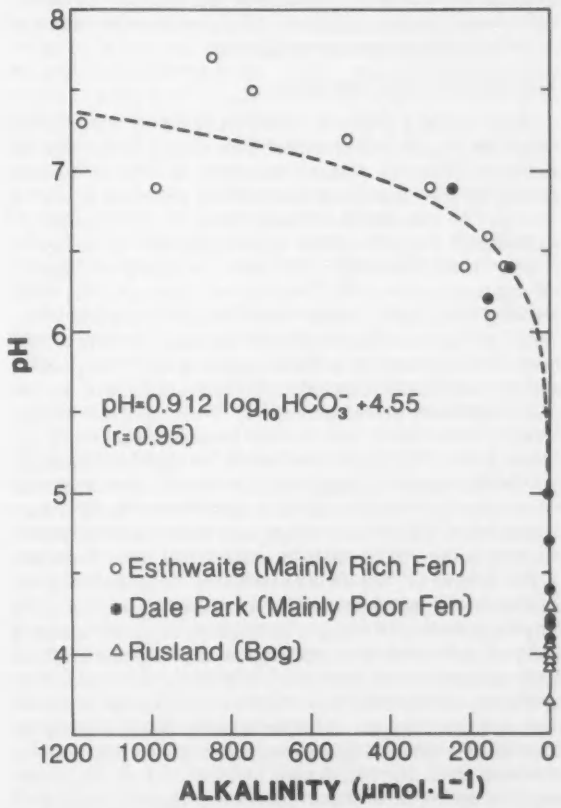

FIG. 1. Relationship between pH and alkalinity in surface waters from fen and bog sites in the English Lake District (regression for 15 waters with some bicarbonate present). Data from Gorham (1956a).

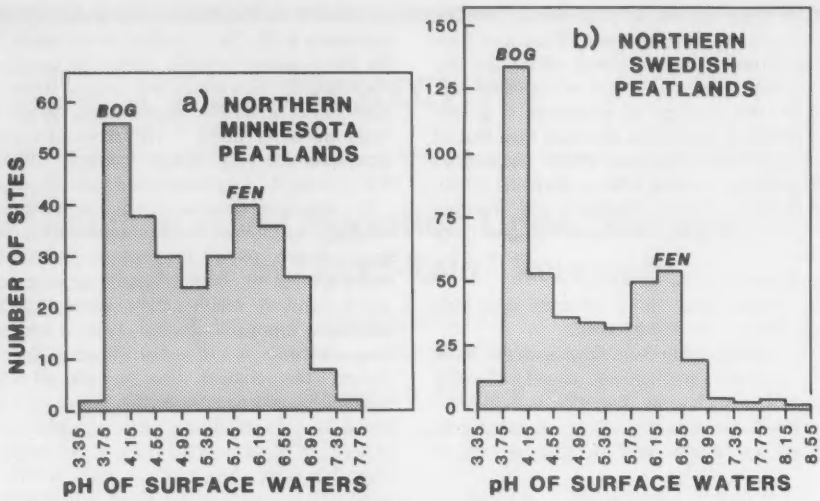

FIG. 2. Frequency distribution of pH in surface waters collected from the different plant communities of peatlands in (a) northern Minnesota and (b) northern Sweden. Minnesota data from E. Gorham, P. H. Glaser, and J. A. Janssens (unpubl.); Swedish data from Sjörs (1952).

chemical and biological responses of peatlands to both natural and anthropogenic acidification. We present here an outline of the problems that require investigation.

The Acidification Process

Many northern peatlands, particularly those ombrotrophic *Sphagnum* bogs that receive all of their mineral inputs from the atmosphere, become acidified naturally. In order to separate natural from anthropogenic acidification processes it will be necessary to examine the balance between organic acids — including the polygalacturonic acids synthesized by *Sphagnum* (Clymo 1963; Spearing 1972) and the complex "humic" substances (Leenheer 1981; Thurman and Malcolm 1981, 1983) resulting from organic decay — and strong mineral acids. This should be done in similar peatland communities over a wide range of acidic deposition from the atmosphere. The possible utility of models that relate pH to nonmarine calcium or calcium plus magnesium (Henriksen 1979, 1980) and the balance between these metal cations and bicarbonate and sulphate (Almer et al. 1978; Wright 1983) should be examined, although the variable cation-exchange capacity of peats may render the relationship less clear than in lake waters. Moreover, Henriksen assumed that systems are in steady state with respect to sulphur; this may not be true owing to the influence of redox reactions.

The fates of all "acidifying substances" deposited from the atmosphere to peatlands must be considered, because it is not only the deposition of strong acids that can cause acidification of ecosystems. For example, metal cations in precipitation that are removed from surface waters by bog plants will be replaced by hydrogen ions from the plants. Likewise, deposition of ammonium sulphate from the atmosphere causes acidification if the ammonium is removed by growing plants. Conversely, removal of anions other than bicarbonate by biological processes may consume hydrogen ions and thus buffer against acidification (National Research Council 1981; Schindler et al. 1980b; Cook and Schindler 1983; Schindler and Turner 1982; Kelly et al. 1982). Indeed, Braekke (1981a) found that peatlands were more efficient sinks for sulphate, nitrate, and hydrogen ion than any of the terrestrial ecosystems that he studied. The net change in the balance of cations versus anions in precipitation, as it passes through a peatland from the atmosphere (or from upland inflow) to the outlet, will determine whether that peatland will become more or less acid. To date, the only published balance has shown that hydrogen ions have been consumed in pore-waters well below the water table in a New England peatland (Hemond 1980). Such studies must be done at different degrees of atmospheric deposition, and at several depths in the peat profile as well as in peat pools, in order to allow reliable extrapolation to other sites and depths.

All of the processes mentioned are known to occur in peatlands, where anoxia and reducing conditions are common below the water table and favour microbial reduction (Howarth and Teal 1979; Hemond 1980; S. E. Bayley, unpubl. data). However, data are insufficient to judge the relative importance of these processes for acidification in a variety of bog types. Although Gorham (1958a) found that the acidity of bog surface waters increased as one approached industrial centers in Britain, Hemond (1980) found that a peatland at a New England site receiving heavily polluted precipitation was able to neutralize the total deposition of acidifying substances, at least after the precipitation had percolated well below the water table into an anaerobic environment where sulphate reduction was possible. Investigation of ion balances in stratigraphic profiles of peat pore-waters, and mass-balance studies of peatland ecosystems (Fig. 3), should be of great value in establishing the degree to which nutrient uptake and microbial reduction can mitigate acidification processes. Such studies are presently underway in a black spruce–*Sphagnum* peatland in northern Minnesota (S. J. Eisenreich et al., University of Minnesota, Minneapolis, MN, pers. comm.). Mass-balance studies are also underway in northwestern Ontario (S. E. Bayley and D. W. Schindler).

The possibility of seasonal reduction of sulphate, followed by reoxidation during dry-weather drawdown of the water table, must also be considered. Evidence suggesting such a process

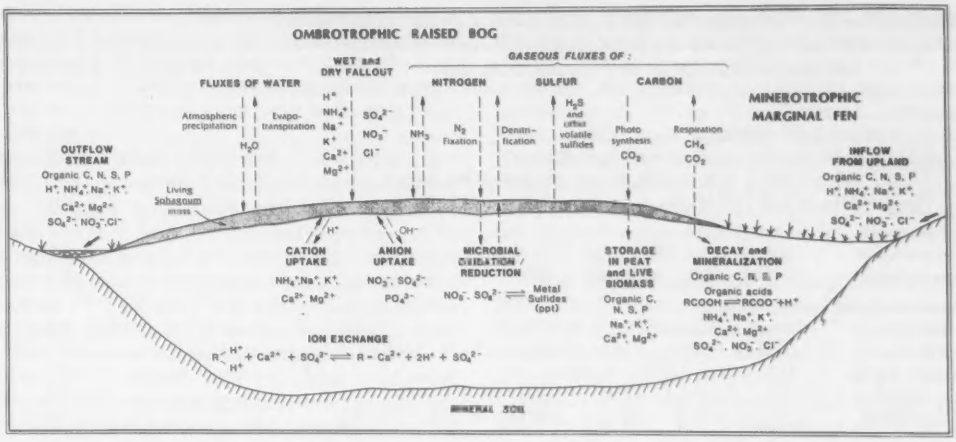

FIG. 3. Ecosystem processes and the pathways of chemical inputs and outputs in an idealized peatland (cf. Hemond 1980).

has been found in bogs (Gorham 1956b; Gorham and Cragg 1960) as well as in terrestrial Norwegian ecosystems and in lakes.

In waters receiving drainage from mineral soils, aluminum hydroxides can be significant buffers in the range of pH 4–5 (Johannessen 1980). However, many peatlands in and below this pH range are raised ombrotrophic *Sphagnum* bogs isolated by several metres of peat from surrounding and underlying soil, so that their mineral supply comes entirely by atmospheric deposition. Aluminum will be supplied to these bog surfaces largely by dry fallout of blown soil dust, and based on several large-scale studies of precipitation chemistry, one would not expect a great deal of buffer capacity from such dustfall (unless of course it includes calcareous loess, cf. Gorham 1976). In British bogs, where there is little dustfall because of the moist climate, acid sulphate loading from anthropogenic sources can reduce the pH in surface pools from as high as 4.5 in remote areas to as low as 3.2 close to large cities (Gorham 1958a).

The cation-exchange complex is another source of buffer capacity in the peat. Cation-exchange capacity is function of organic content and degree of decomposition (Gorham 1967). In fens receiving much of their water from the mineral soil, hydrogen ions deposited from the atmosphere will be subject to exchange with a much larger reservoir of metal cations adsorbed on the peat colloids (Gorham 1967). In bogs, receiving only atmospheric inputs of mineral material, the peat exchange complex — derived largely from polygalacturonic acids synthesized by *Sphagnum* moss (Knight et al. 1961; Clymo 1963; Spearing 1972) — is already strongly saturated (approximately 75–98%) by hydrogen ions (Gorham 1953b; Sjörs 1961; Braekke 1981b), so that hydrogen ions deposited from the atmosphere are much less likely to be replaced by exchange with adsorbed metal cations. Cation-exchange capacity is dependent upon the nature of the saturating cation and on the nature and pH of the displacing solution; capacity declines sharply as the pH is lowered (Clymo 1983).

Recent studies of the chemistry of bog waters from Manitoba to Newfoundland (Gorham et al. 1984) have shed additional light upon the acidification of surface waters in ombrotrophic bogs. These investigations indicate that the biological production of filter-passing organic acids can lead to pH values in surface bog waters within the range 3.7–4.7 despite the biological reduction of sulphate concentrations in these waters to an average of 18 $\mu eq \cdot L^{-1}$ (range, undetectable to 81 $\mu eq \cdot L^{-1}$), well below the concentrations of 50–100 $\mu eq \cdot L^{-1}$ observed in atmospheric precipitation (which would otherwise be considerably increased by evapotranspiration from the bog surfaces). Nitrate and ammonium ions, also highly relevant to the acidification process, are usually reduced in surface bog waters to a few $\mu eq \cdot L^{-1}$, far below the levels of atmospheric precipitation. However, Gorham et al. (1984) have also shown that where acid deposition is severe, the acidity of bog waters can be dominated by strong mineral acid. Two bogs subject to severe air pollution in the southern Pennine Mountains of England provide an example; their waters are very low in coloured, filter-passing organic matter but high in hydrogen ions (mean 160 $\mu eq \cdot L^{-1}$) and especially in sulphate (mean 273 $\mu eq \cdot L^{-1}$).

The reduction processes mentioned as taking place in bog waters presumably operate also in fens. However, fens collect water from the surrounding uplands, causing more rapid water rates of water flow and higher chemical inputs than bogs (cf. Hofstetter 1969). While increased water renewal should lessen the effects of sulphate and nitrate reduction upon the chemistry of fen waters, increased chemical inputs would tend to increase these processes. This question is obviously of great importance as regards the postulated influence of acid deposition in triggering the invasion of poor fens by acidophilic *Sphagnum* mosses. In this connection, Sparling (1966) has shown an increase of pH in Ontario fens from between 5.1 and 5.6 at flow rates of about 0.1 $cm \cdot s^{-1}$ to between 5.6 and 6.0 at rates of about 8 $cm \cdot s^{-1}$. The influence of velocity appeared to be distinctly greater in those waters poorer to bases. On the other hand, Vitt and Bayley (1984) have found that a high proportion of incoming sulphate is reduced in both bogs and fens, irrespective of sulphate input or pH.

It is of interest that fens whose waters are in the critical range around pH 6 exhibit quite high degrees of base saturation (> 60%) on the cation-exchange complexes of the top 5–10 cm of their peats (Gorham 1953b; Sjörs 1961). Presumably only those basic metal cations adsorbed close to the very surface of fen peat are readily available for exchange with hydrogen ions

TABLE 1. Processes that alter the hydrogen ion balance in the waters of peatlands (after Stumm et al. 1983).

Alteration in alkalinity per mole reactant (underlined)	Δ (Alk) = −Δ (H-Acid) (eq·mol^{-1})
Weathering reactions	
(1) $\underline{CaCO_3(s)} + H^+ \rightleftharpoons Ca^{2+} + HCO_3^-$	+2
(2) $\underline{CaAl_2Si_2O_8(s)} + 2H^+ \rightleftharpoons Ca^{2+} + H_2O + Al_2Si_2O_5(OH)_4(s)$	+2
(3) $\underline{KAlSi_3O_8(s)} + H^+ + 4\frac{1}{2}\,H_2O \rightleftharpoons K^+ + 2H_4SiO_4 + \frac{1}{2}Al_2Si_2O_5(OH)_4(s)$	+1
(4) $\underline{Al_2O_3{\cdot}3H_2O} + 6H^+ \rightleftharpoons 2Al^{3+} + 6H_2O$	+6
Ion-exchange processes	
(5) Cation exchange $NaR + \underline{H^+} \rightleftharpoons HR + Na^+$	+1
(6) Anion exchange $2ROH + \underline{SO_4^{2-}} \rightleftharpoons R_2SO_4 + 2OH^-$	+2
Redox processes (mediated by microbes)	
(7) Nitrification $NH_4^+ + 2O_2 \rightleftharpoons NO_3^- + H_2O + 2H^+$	−2
(8) Denitrification $\underline{5CH_2O} + \underline{4NO_3^-} + 4H^+ \rightarrow 5CO_2 + 2N_2 + 7H_2O$	+1
(9) Oxidation of H_2S $\underline{H_2S} + 2O_2 \rightarrow \underline{SO_4^{2-}} + 2H^+$	−2
(10) SO_4^{2-} reduction $\underline{SO_4^{2-}} + 2CH_2O + 2H^+ \rightarrow 2CO_2 + H_2S + H_2O$	+2
(11) Pyrite oxidation $\underline{FeS_2(s)} + 3\frac{3}{4}O_2 + 3\frac{1}{2}H_2O \rightarrow Fe(OH)_3 + 2SO_4^{2-} + 4H^+$	−4
Synthesis (→) and decomposition (←) of biomass and of humus	
(12) Photosynthesis with NO_3^- assimilation (→), aerobic respiration (←) $aCO_2(g) + bNO_3^- + cHPO_4^{2-} + dSO_4^{2-} + \ldots + gCa^{2+} + hMg^{2+} + iK^+ + fNa^+ + xH_2O$ $+ (b + 2c + 2d - 2g - 2h - i - f)H^+ \rightleftharpoons \{C_aN_bP_cS_d \ldots Ca_g\,Mg_h\,K_i\,Na_f\,H_2O_m\}_{biomass}$ $+ (a + 2b)O_2(g)$	$a{\cdot}0 + b + 2c + 2d - (2g + 2h + i + f)$
(13) NH_4^+ assimilation (→), anerobic mineralization (half-reaction) (←) $aCO_2(g) + bNH_4^+ + \ldots \rightleftharpoons \{C_a \ldots N_b \ldots\}_{biomass} + aO_2(g)$	$a{\cdot}0 - b$
(14) N_2 fixation (half-reaction) $\ldots + b/2\,N_2(g) + \ldots \rightarrow \{\ldots N_b \ldots\}_{biomass}$	$b{\cdot}0$

generated either naturally by the growth and decay of bog mosses or by acid deposition from anthropogenic sources. Possibly, leaching the top 1–2 cm of a fen peat to a point where the surface waters are in the critical pH and alkalinity range may greatly favour, and even trigger, the invasion of *Sphagnum* mosses that have a strong ability to acidify their surroundings further, particularly as hummock-forming species (e.g. *S. magellanicum* and *S. fuscum*) succeed the initial carpet formers (e.g. *S. recurvum* agg. and *S. papillosum*) that begin to raise the peat surface above the level of minerotrophic groundwater. The rapid acidification of minerotrophic sites by *Sphagnum* will involve not only the soluble fulvic acids that are the major products of organic decomposition (H. F. Hemond, Department of Civil Engineering, MIT, pers. comm.), but more importantly the much more abundant hydrogen ions adsorbed on the polygalacturonic acid cation-exchanger in the cell walls of the moss. In wet climates the acidifying potential of *Sphagnum* may lead to the development of acid peat only a few centimetres above limestone (Webb 1947).

To sum up, the chemical and ecological effects of acid precipitation depend directly on the hydrogen ion activity in rain and snow with associated anions *and* the net changes in alkalinity or buffering capacity resulting from interaction with the plants and the peat. The processes that modify the hydrogen ion balance in peat and pore-water are shown in greater detail in Table 1 (see also Fig. 3). The processes that play the most prominent roles in controlling alkalinity or buffering are the cation-exchange reactions with surface peat, redox processes at and below the water table, and interaction with water-soluble organic matter, composed largely of fulvic and uronic acids. Careful examination of these reactions as a function of depth should allow us to understand the processes governing the response of peat systems to incoming hydrogen ions in precipitation.

Control of Nutrient Availability

The natural process of peatland acidification that accompanies the replacement of minerotrophic fen by ombrotrophic bog communities in the course of peatland succession (Walker 1970) causes a striking decline in the percent saturation by metal cations of the ion-exchange complexes in the peat (Gorham 1953b, 1967; Sjörs 1961). A low degree of base-saturation poses a severe problem for plants in the uptake of adsorbed nutrient cations such as calcium, magnesium, potassium, and ammonium, because in a given volume of peat most of these nutrient cations are in the adsorbed rather than the solution phase (Gorham 1967; Clymo 1983). Exchange of nutrient cations on the peat exchange complex for hydrogen ions generated at root surfaces is difficult if the peat exchange complex is already saturated (up to 98%) by hydrogen ions. Increased atmospheric deposition of strong acids is likely to worsen the already extremely oligotrophic conditions for growth in such sites.

Differences in acidity can also affect the availability of anionic nutrients. Phosphate adsorption by anion-exchange complexes is strongly influenced by pH, which may also affect processes such as nitrification, denitrification, and nitrogen fixation (National Research Council 1981).

The role of ion exchange in the nutrition of peatland plants could be of great importance in relation to effects of acid deposition, and it deserves investigation over a broad range of peatland sites under various deposition regimes.

Mobilization of Metals

The increased mobilization of toxic metals (e.g. aluminum, mercury, zinc, copper, lead, cadmium) by ion-exchange and weathering from soils and sediments as pH declines is another aspect of acidification that requires study.

Mobilization of metals by acidification is well known both in lakes (Dickson 1980; Schindler et al. 1980a) and in upland areas (Cronan and Schofield 1979), and it is logical to expect the same processes to occur in wetlands. In lakes, inorganic and organic binding of metals in sediments occur, and both seem to be affected by low pH.

Iron and manganese are mobilized both by low pH and low redox potential (E_h). As a result, a number of trace metals that are normally scavenged by insoluble precipitates of ferric or manganese dioxides (e.g. lead, barium, molybdenum) can be liberated by acidification or by the low redox potentials that normally accompany anoxic conditions. Several fallout radionuclides, such as ^{239,240}Pu and ^{137}Cs, are similarly related to iron and manganese (Alberts and Orlandini 1981; Sholkovitz et al. 1983). These processes are well investigated in lakes (cf. Mortimer 1941, 1942; Gorham 1958b; Gorham and Swaine 1965) but have not been studied in peatlands to our knowledge. Damman (1978) and Pakarinen et al. (1981) have shown that the changes in redox conditions that accompany water level fluctuations can have important consequences for the cycles of several metals in bogs.

Organic binding of metals in lake sediments was analyzed in detail by Jackson et al. (1980), who found that from 10 to 40% of several metals (including Hg, Co, Cr, Zn, Fe, Mn, Se) in sediments was bound to humic materials. Fulvic acids and bituminous fractions were less important binding agents. Acidification decreased the capacity of the sediments to bind most of the metals. Although no detailed study of metal-binding mechanisms in peatlands has been made, the association of 10 trace elements in six suspended and dissolved fractions of swamp water from the Okefenokee was studied by Giesy and Briese (1977) (see also Alberts and Giesy and others in Christman and Gjessing 1983). The association between metals and organic matter in filter-passing fractions is well known for coloured bog water (Forstner and Wittman 1979). Bog mosses and peats are also known to accumulate high concentrations of metals such as lead, cadmium, and zinc from polluted precipitation (Rühling and Tyler 1971; Pakarinen and Tolonen 1976; Damman 1978; Livett et al. 1979; Braekke 1981b). The last-named author noted that high zinc concentrations occurred deeper in peat profiles than could be accounted for by precipitation alone, and he interpreted this as evidence for mobilization and downward movement of the element. Construction of a reservoir in northern Manitoba flooded large areas of boreal forest and peatland, mobilizing large quantities of mercury that subsequently accumulated in fish. Peatlands were found to be the most important source of the element (Bodaly and Hecky 1979; Bodaly and Hecky, Department of Fisheries and Oceans, Winnipeg, Man., pers. comm.). Jackson and Hecky (1980) demonstrated the effects of flooding on micronutrient cycling.

Overall, there seems to be reason to expect that further acidification of peatlands may cause increased releases of several toxic metals to downstream waters. Mobilization may be greatest in floristically poor fens that are below pH 6.0 but have sufficient mineral matter (silt and clay) intermixed with the organic peat to provide good sources of metals.

Effects on Biogeochemical Cycling by Fauna and Microflora

A very important facet of the cycling of nutrients and toxins is the activity of the peat fauna (Coulson and Whittaker 1978) and microflora (Collins et al. 1978) that are engaged in the decomposition of organic carbon to carbon dioxide and methane (Clymo and Reddaway 1972; Harriss et al. 1982). The microflora also performs a variety of other biogeochemical transformations (Given 1975; Given and Dickinson 1975). These include such important tasks as sulphate reduction (Connell and Patrick 1968; Hemond 1980), nitrogen fixation (Waughman and Bellamy 1980; Blasco and Jordan 1976), denitrification (cf. Chan and Campbell 1980), and the methylation of mercury and other elements (cf. Wood 1974; Furutani and Rudd 1980).

The distribution of various microorganisms in relation to the pH and E_h of different types of bog and fen habitats (cf. Pratt and Gorham 1970; Gorham and Pratt 1972; Burke et al. 1974) has seldom been investigated. Examination of the linkage between microbiology and the biogeochemistry of peatlands is not far advanced (Given and Dickinson 1975; Dickinson 1983; Sikora and Keeney 1983), and the influence of acidification upon that linkage is not well known. However, by analogy with lake studies we may expect both increased activity of sulphate reducers (Schindler et al. 1980b) and the transformation of mercury into the toxic mono-methyl form that accumulates in fish (Tomlinson et al. 1980).

Effects on Receiving Waters

An important consideration in both the natural and the anthropogenic acidification of peatland is the possibility that peatland outflow may discharge acid and mobilized toxic metals to the streams and lakes into which they drain. Tea-coloured bog lakes, ponds, and streams are a common feature of the Precambrian Laurentian Shield and similar landscapes elsewhere. For example, according to Lillie and Mason (1983), 38% of a random set of 560 lakes in Wisconsin, chiefly in the northern half of the state, were rated as brown in colour. Waters already acidified naturally to some degree by bog drainage may be particularly liable to reach toxic pH levels when they are subject to acid deposition from the atmosphere.

Dissolved aluminum in acidic streams may also precipitate after entry to a lake, scavenging phosphorus as it does so (Dickson 1980). In this way the dynamics of a major nutrient can be affected.

The Significance of Hydrology

Hydrological studies will be important in examining the acidification of peatlands. For instance, acid pulses may occur not only at snowmelt and during large precipitation events (cf. Galloway et al. 1980) but also during drawdowns — either seasonally (Gorham 1956b) or after periods of drought (Hultberg and Wenblad 1980; Braekke 1981c). At such time, aeration of normally anoxic soils and peats may oxidize organic sulphur, or metallic sulphides precipitated in the reduced form, to sulphuric acid (cf. Wiklander and Hallgren 1949; Wiklander et al. 1950a, 1950b). As mentioned earlier, associated effects on the mobility of metals also occur (Wiklander and Hallgren 1949; Koutler-Andersson et al. 1955; Damman 1978).

Groundwater movements may be an important factor in determining the complex patterns of natural peatland acidification (Glaser et al. 1981; Siegel 1981). Some peatlands are groundwater recharge areas, whereas others are discharge areas. Because groundwaters normally have some alkalinity,

peatlands in discharge areas will have some capacity to buffer acid deposition. Recharge areas are likely to be much more vulnerable.

Permafrost, a characteristic of northern peatlands, may be a significant factor in acidification insofar as it restricts the volume of peat accessible to acid deposition. Water flow in peatlands is largely confined to the surface "active layer" (Goode et al. 1977; Gorham and Hofstetter 1971), so that the deeper pore-waters, even if minerotrophic, are unlikely to be very significant as a reservoir of neutralizing alkalinity, or of mobile metals.

In catchments composed of both terrestrial and peatland ecosystems, the latter contribute disproportionately to the loss of water, and thereby of dissolved materials. For example, at a catchment in Storgama, Norway, Braekke (1981a) found that 62% of the output water was chemically altered by flow through the peatlands although they constituted only 24% of the surface area of the catchment.

Drainage of peatlands can cause severe acidification as reduced sulphur is reoxidized. At present the total area of peatlands drained for forestry and agriculture amounts to more than 15 million ha, with a yearly increase of about 0.5–0.6 million ha (Kivinen and Pakarinen 1981). During such drainage, or drawdown by drought, many years' deposition of reduced sulphur may be reoxidized in a short time. Heavy anthropogenic emission and redeposition of sulphur must increase the potential for rapid peatland acidification during drainage or drawdown, as it has in Swedish groundwaters (Hultberg and Wenblad 1980).

Biological Responses to Acidification

The responses of peatland organisms to acidification (and to the nutrients and toxic metals that accompany acid deposition) can be examined at a number of different levels in much the same way as organisms in the more intensively studied aquatic and terrestrial ecosystems (Drablos and Tollan 1980; Overrein et al. 1980).

Individual Species of Plants and Animals

Individual plant and animal species must be investigated with regard to growth, reproduction, and health at biochemical, physiological, and ecological levels, as has been done extensively with some lacustrine fish and invertebrates (e.g. Muniz and Leivestad 1980; Malley 1980; Kennedy 1980). In addition, the dynamics of plant and animal populations (cf. Beamish 1974; Glass and Loucks 1980), and the selection of acid-tolerant strains within such populations (cf. Stokes et al. 1973), should be studied.

Many peatland plants are likely to be susceptible to acid deposition. Even several distinctly acidophilous species of *Sphagnum* have almost entirely disappeared from the large blanket bogs of the southern Pennines in Britain (Tallis 1964), subject for many decades to extreme acidification (Gorham 1958a). The virtual extinction of *Sphagnum* from these areas is almost certainly a result of atmospheric pollution in Britain for the last 150 yr. Loss of these species has made the bogs more susceptible to erosion (Tallis 1964), and effects on water quality downstream would be expected. It is impossible to say with certainty that the loss of species is caused by acid precipitation because this disappearance occurred over a period of 150 yr. Acid precipitation is known to have occurred in central Britain for well over 100 yr (Smith 1852). Recent experiments by Ferguson et al. (1978) have shown that the same species of *Sphagnum* studied by Tallis are susceptible to both acid rain and sulphur dioxide fumigation. Growth, measured by length of shoot, chlorophyll content, and photosynthetic carbon fixation, was inhibited by various application rates of HSO^{3-}, SO_4^{2-}, and SO_2 within the range of concentrations detected in British precipitation. Low applications of these chemicals stimulated growth.

By analogy with organisms in other ecosystems, the susceptibility or resistance of peatland organisms to infection and disease is also likely to be influenced by the acidity of their substrates. In lakes, for example, decreasing the pH greatly increased fungal infection of the egg masses of crayfish (France 1982). Microsporozoan infections of crayfish also increased. Peatland tree species such as tamarack (*Larix laricina*) and black spruce (*Picea mariana*), which grow over a wide range of environmental conditions, would be obvious candidates for study of the relationship between substrate pH and the prevalence of needle rusts, root rots, cankers, and infections by dwarf mistletoe. In this connection, some degree of soil acidity may reduce the incidence of disease. For instance, a pH of just above 5 is optimal for prevention of fungal attack upon conifer seedlings from germination to early emergence (Boyce 1948).

The stem increments (ring widths) of peatland trees can be used as an index of general vigor and of growth response to nutritional factors. In combination with "site-index" measurements of age-specific tree heights, they deserve analysis along natural or anthropogenic gradients of substrate acidity. Controlled experimental acidification could also prove valuable in this connection.

The study of growth rings in trees points up a major complication that must continually be borne in mind in all studies of biological response to peatland acidification. Plant growth in peatlands is susceptible to the fluctuations in water table that occur in response to variations in climatic factors from year to year. In Minnesota, for example, both tamarack and black spruce exhibited sharply increased widths of annual rings during the drought of the 1930's (Hofstetter 1969; Tilton 1975), presumably because of better root aeration and increased mobilization of nutrients from the peat by a more active aerobic microflora. It is likely that disentangling growth responses to acidification from climatic "noise" imposed upon the ring width record will be very difficult, especially where drought enhances acidification, as we have described. Moreover, many other species of plants and animals are probably responsive to fluctuations in moisture. Clymo (1973) has shown experimentally a strong effect on various species of the bog moss *Sphagnum*; in this case the response to decreasing moisture was negative.

Responses of populations of animals other than fish to acidification have not been well-studied. Pough (1976) found that acid conditions inhibit the survival of embryos of two species of the salamander *Ambystoma*. Nyholm (1981) found that the eggshells of the pied flycatcher (*Ficedula hypoleuca*) in acidified areas were fragile and high in aluminum. High aluminum concentrations were also found in bone marrow. Clutches that hatched were small. The author postulated that excess aluminum was accumulated from feeding on insects that emerged from acidified sediments.

Plant and Animal Communities

Extensive analysis of peatland floras and faunas reveals

marked changes in the nature of both plant and animal communities along natural gradients of acidity in peatlands. In northwestern Minnesota, for example, stands of the sedge *Carex atherodes* occupy alkaline to circumneutral silty peats in many prairie wetlands, whereas stands of *Carex lacustris* are observed on circumneutral and more organic peats in the adjacent forests. *Carex lasiocarpa* meadows with or without *Sphagnum* carpets occur on more oligotrophic, circumneutral to moderately acid peats, often as floating mats around small ponds in the forest zone. *Carex oligosperma* meadows with *Sphagnum papillosum* carpets occupy acid and highly organic peats in the floristically poor fens that are transitional to the extremely acid raised *Sphagnum* bogs of the Red Lake Peatland.

Each of the above communities has its own distinct flora and fauna, although many species are wide-ranging and occur in more than one of them. Studies of acidification response should, however, focus on those plants and animals with narrow pH ranges that are "indicator species" or make up "indicator communities." In this connection, bryophytes are often more sensitive indicators of acidity than are vascular plants; many microalgae are probably also highly sensitive (Du Rietz 1950a, 1950b, 1950c; Merilainen 1967; Munsch 1980; Renberg and Hellberg 1982). Some of the vascular plants can root deeply where conditions are less acid than in the material accumulating on the present surface of the peatland, so that they exhibit a sort of "biological inertia" in the face of changing conditions (Gorham 1957). Small invertebrates are similarly likely to be better indicators of habitat pH than large and more migratory mammals and birds; for example, snails are closely restricted to local, circumneutral substrates.

The concept of indicator species within plant or animal communities is an old and very useful one (Watson 1833; Gorham 1954; Thomas 1972) that may assist in determining the degree of natural or anthropogenic acidification of a given peatland. However, it must be employed with caution and without too much geographical extrapolation. For instance, many species that are indicators of weakly minerotrophic, floristically poor fen communities in continental peatlands are observed in distinctly more acid, ombrotrophic bog communities in maritime areas. Some peatland species are even more extreme. For instance, the black bog rush, *Schoenus nigricans*, is a calciphile on the continent of Europe and in southeastern England although it is extremely acid-tolerant in western Ireland. Such situations are well known in Europe (Gorham 1956b) and have been observed recently in North America (Damman 1979). To take one example, *Carex exilis* is rare and restricted to minerotrophic fens in Minnesota, whereas it is a common plant in ombrotrophic bog communities in the Maritime Provinces of Canada (P. H. Glaser and M. V. Santelmann, Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, MN, pers. comm.). Whether ecotypic differences exist in such disparate populations is not known, but the matter is presently under investigation (M. V. Santelmann, pers. comm.).

Ecosystems

The structural properties of whole ecosystems — vegetation life forms, indices of floristic and faunistic dominance, diversity or similarity, and food webs — may all vary in relation to substrate acidity and respond to natural or anthropogenic acidification. Such variation could probably be synthesized effectively into a few composite variables that reflect environmental gradients by using multivariate statistics. As yet, the responses of the structural properties of wetland ecosystems to acidification have not been seriously investigated, although much could probably be learned by a synthesis of the diverse literature on natural pH gradients.

Functional properties of ecosystems also respond to gradients of acidity. For instance, the accumulation of peat into domed raised bogs is a process partly reflecting climatic moisture regime (Granlund 1932; Kulczynski 1949; Wickman 1951) and partly associated with acidification (Gorham 1949, 1953b; Mattson and Koutler-Andersson 1954). The process results from an excess of production over decomposition, both being generally low on acid substrates that are poor in nutrients.

When whole ecosystems may be at hazard, it is important to determine whether there are indicators that give early warning of damage by acid deposition or other anthropogenic stresses. The loss of one species may be counterbalanced by an increase in the population of another that takes over its niche and function in the ecosystem, so it seems likely that floristic and faunistic changes will be far more sensitive in providing such an early warning than changes in rates of productivity, decomposition, and other ecosystem functions. This is already known to be the case in acidified lakes (Henrikson et al. 1980; Schindler 1980; Schindler and Turner 1982).

Peatlands as Possible Sources of Acid-Rain Precursors

Because of the anoxic character of peatland soils beneath the water table, volatile compounds of sulphur are produced by microbial reduction in peatland habitats where sulphate is abundant. If emitted to the atmosphere these compounds can be oxidized, ultimately to sulphuric acid (Hitchcock et al. 1980; Charlson and Rodhe 1982). However, it has been shown that sulphide can be precipitated by ferrous iron in peatlands where the latter is plentiful (Howarth and Teal 1979; S. E. Bayley, unpubl. data). In such situations the sulphur would not enter the atmospheric cycle. The importance of peatlands as sources of atmospheric sulphur is almost unknown (National Research Council 1981), but they could be significant for the biogenic part of the global sulphur cycle. Nitrogen oxides (and ammonia) may also be emitted from peatland soils owing to microbial metabolism.

Clearly, natural sulphur and nitrogen emissions in northeastern North American and northern Europe are of minor significance in comparison with the anthropogenic emissions that are the cause of the severe "acid-rain" problem in those areas (Galloway and Whelpdale 1980; Gorham 1984), but they may play a part in producing occasional acidic rainfalls in remote areas (cf. Galloway et al. 1982). The extensive areas of salt marsh, fen, and bog in the remote Hudson Bay Lowlands (Sjörs 1959; Zoltai 1980; Anonymous 1981) would provide ideal ecosystems for the investigation of natural emissions of volatile compounds of sulphur and nitrogen, to see how far these vast wetlands may contribute to the acidity of precipitation either locally or via long-range transport. A point to consider in this connection is whether there may be appreciable reemission from wetlands of sulphur and nitrogen compounds deposited from the atmosphere after long-range transport from anthropogenic sources. Stable isotope ratios might be a useful tool in studying this question (cf. Nakai and Jensen 1967; Nriagu and Coker 1983).

Different Approaches to be Employed

The study of peatland acidification will necessarily involve a variety of approaches.

Geographical Surveys

Three sorts of investigations are desirable. Initially, the vulnerability of a range of peatland habitats to acid deposition should be examined in an area so far little affected by it. Such a study would focus on describing the nature of the plant and animal communities in circumneutral fens and naturally acidified bogs, and analyzing the chemistry of surface pools, pore-waters, and exchangeable ions in the peat. Representative plants and animals might also be analyzed for a variety of chemical elements. The susceptibility of the waters and peats in these communities to acid deposition would also be measured. Waters would be titrated (cf. Fig. 1), whereas short peat cores would be leached by acid in a standard fashion, after which the effluents would be titrated and analyzed for major ions and trace metals.

Next (or at the same time), the responses of different types of bog and fen to acidification would be compared within a single geographical area subject to considerable (and well monitored) acid deposition. As remarked earlier, floristically poor fens with waters in the vicinity of pH 6 might well be most susceptible.

The third approach would involve comparing specific peatland types (for instance, the above-mentioned poor fens) across geographical gradients of acid-loading, say from Minnesota and Manitoba through Ontario and New England to the Maritime Provinces of Canada and Labrador. Present monitoring networks (CANSAP/CAPMoN, NADP) could provide appropriate data on acid deposition, although local monitoring would also be important.

Experimental Approaches

The observational approaches just described should be followed by experimental acidification of selected habitats to confirm conclusions drawn from observation, and also to examine the subtle detailed changes in community composition, biogeochemical cycling, and general metabolism that cannot readily be inferred from comparative observations because of inevitable variations among the sites being compared. Once again, floristically poor fens might be of most interest. Such an experimental approach has proven to be of great value in the study of lake acidification (Schindler et al. 1980a, 1980b; Schindler and Turner 1982) and of the responses of forest soils to acidification (Abrahamsen 1980; Overrein et al. 1980).

Radioactive and stable isotopes should be of considerable value in working out biogeochemical cycles in peatlands. Radioisotope experiments to elucidate gaseous metabolism (Stuiver 1967) and the cycles of carbon and metals (Hesslein et al. 1980a, 1980b; Schindler et al. 1980a) in lakes, and studies of the retention of $^{35}SO_4$ and ^{45}Ca in small terrestrial catchments (Seip 1980; Overrein et al. 1980), provide models for future peatland studies. Analysis of the ratios of stable sulphur isotopes may provide information concerning microbial activity in peats (cf. Nakai and Jensen 1964) and the changing balance of natural and anthropogenic sulphur in peatlands over time (cf. Nakai and Jensen 1967). Braekke (1981b) noted that in peatlands there was normally a net release of sulphate during July–September and net uptake during the rest of the year. However, this pattern is not observed in the Marcell black spruce–*Sphagnum* peatland in northern Minnesota (S. J. Eisenreich, Department of Civil and Mineral Engineering, University of Minnesota, Minneapolis, MN, pers. comm.). Seasonal patterns are attributable to effects of water level fluctuation on reduction and oxidation of inorganic and organic forms of sulphur. The possibility that acidification could affect biological processes of isotope fractionation requires investigation.

Time Scales

The initial geographical studies will inevitably involve short-term comparison of diverse sites. They should be supplemented by long-term chemical and biological monitoring of selected sites to establish secular trends of acidification and response. Such monitoring could benefit greatly by prior or concurrent paleoecological investigations, in which stratigraphic examination of peat cores is employed to measure changes in a variety of ecosystem properties (cf. Mattson and Koutler-Andersson 1954; Wright et al. 1963; Watts and Winter 1966; Walker 1970; Sanger and Gorham 1972). Fossil assemblages (e.g. of pollen, seeds, leaves, twigs, bryophyte remains, rhizopod tests, insect remains, plant pigments, etc.) and chemical properties (e.g. carbonate content, clay mineralogy, percent base saturation, concentrations of calcium, iron, aluminum, lead, etc.) can be of great value in determining patterns of change prior to the onset of monitoring. They can also be very important in establishing the comparability of different locations. For example, where matching control and experimental sites are sought, there is seldom sufficient time to establish comparable ranges of fluctuation in ecosystem characteristics, because 10 yr or more of study may be required. In such a situation paleoecological analysis can be extremely useful. For peatlands, paleoecological studies of bryophytes are likely to be especially useful (Janssens 1983).

Mass-Balance Studies

As reviewed earlier, several internal and external processes can affect the acid–base balance of peatlands. The net effect of these can be seen only by comparing the outflow chemistry with that of atmospheric deposition and the inflow from surrounding uplands (Fig. 3). Such studies will be impossible in large peatlands owing to inadequate hydrological control. Small peatlands with outflow streams, such as those in much of the southern and western Precambrian Shield (Boelter and Verry 1977), will be the most appropriate sites for these studies.

Peatlands in the Acidified Landscape: The Need for an Inclusive Approach

Initially, the investigation of peatland acidification should be focussed upon the peatlands themselves, perhaps upon a single type such as poor fen. However, peatlands obviously can have a significant influence upon the streams and lakes into which they drain. For example, Schindler et al. (1976) found that, for 9 of 12 elements studied, an Ontario catchment consisting largely of a black spruce peatland had higher yields per unit area than two adjacent upland catchments (Table 2). Discharge of trace metals from this same peatland was also much higher than in the upland catchments, with aluminum and zinc concentrations occasionally approaching values toxic to aquatic organisms (D. W. Schindler, unpubl. data). In Nova Scotia it is likely that the lakes and rivers most susceptible to anthropogenic acidification are those with highly coloured waters that have already

TABLE 2. Average annual yields and standard deviations of several chemical elements from three adjacent streams in the Experimental Lake Area, northwestern Ontario. Units are $kg \cdot ha^{-1} \cdot y^{-1}$. Data for the years 1970–73 from Schindler et al. (1976). All but the underlined yields are greatest in the northeast (bog) drainage basin. The stream from the northwest sub-basin also has higher dissolved organic carbon than the east sub-basin.

	Sub-basin		
	Northwest	East	Northeast (bog)
Mean pH	5.20	6.12	4.68
H^+	0.018 ± 0.008	0.0037 ± 0.0034	0.081 ± 0.016
P	0.04 ± 0.02	0.05 ± 0.01	0.08 ± 0.05
N	0.92 ± 0.34	1.02 + 0.04	1.67 ± 0.08
C	58 ± 30	53 ± 7.4	116 + 31
Ca	4.14 ± 1.93	7.24 ± 0.89	5.05 ± 1.01
Mg	1.88 ± 0.77	2.73 ± 0.33	2.18 ± 0.37
Na	2.66 ± 1.14	4.35 ± 0.57	3.72 ± 0.30
K	0.68 ± 0.34	1.49 ± 0.26	1.89 ± 0.66
Si	10.9 ± 3.6	15.3 ± 1.7	16.4 ± 3.8
Cl	0.52 ± 0.30	0.82 ± 0.48	0.95 ± 0.30
Fe	0.58 ± 0.01	1.16 ± 0.12	1.37 ± 0.36

undergone some degree of natural acidification by drainage from peatlands (J. Kerekes, Canadian Wildlife Service, Halifax, N.S., pers. comm.). Because the interaction between peatlands and wholly aquatic ecosystems may be of great importance, for instance, to sport fisheries, it must be examined in some detail. But many fens in turn are greatly affected by drainage from the surrounding uplands and must, like adjacent streams and lakes, receive high concentrations of sulphate, hydrogen ion, calcium, aluminum, and trace metals from soils leached by acid deposition from the atmosphere. Therefore, the ultimate need will be for integrated studies of upland, peatland, and aquatic ecosystems that are linked together within a single catchment subject to acid deposition. No such study has yet been attempted, and no single institution has the resources to mount such an integrated study at the present time.

Conclusion

Because of their possible vulnerability to acid deposition, it is important that peatlands not be allowed to "slip through the cracks" between the mandates of ecological management and research organizations, as has been the case in the past. They are a large and vital part of the landscape in areas vulnerable to acid deposition, forming inseparable linkages with both aquatic and terrestrial ecosystems, and they must not be forgotten!

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LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

On Group Testing for Diseases

Worlund and Taylor's (1983) note on group testing contained a totally inadequate review of the scientific literature. The methodology that they described was previously derived by Gibbs and Gower (1960), Thompson (1962), Sobel and Elashoff (1975), Hoenig (1981), and Hoenig and Lawing (1982).

The idea of pooling or grouping samples in a random way goes back at least as far as 1943 when Dorfman (1943) proposed a mass screening of armed forces inductees for syphilis by combining blood samples. Dorfman's work was followed by numerous studies of optimum group size for initial screening and subsequent retesting of subgroups (see Sobel and Groll 1959; Hoenig 1981).

Gibbs and Gower (1960) and Thompson (1962) proposed the use of group testing for estimation. They derived the maximum likelihood estimator and its asymptotic variance as well as studied the bias and discussed the design of studies. Sobel and Elashoff (1975) considered estimation when positive groups could be broken into subgroups for subsequent testing. We also invented group testing but did not publish the basic idea because of the priority of the above authors. We had to content ourselves with studying ways to design an experiment to avoid a large bias (Hoenig 1981; Hoenig and Lawing 1982).

Our work (Hoenig and Lawing 1982) appeared in a fishery newsletter. A recent review of the subject appeared in *American Statistician* (Loyer 1983). *Current Index to Statistics* lists numerous articles on the subject.

We find few problems with Worlund and Taylor's treatment of the subject. However, the following points should be made (Hoenig 1981):

(1) Individual samples must be randomly assigned to groups in order for the binomial model to apply.

(2) A cost function was incorporated into our procedure for choosing optimal testing conditions.

(3) Optimal value of group size, k, is only asymptotically independent of the number of groups. We treated the small sample case.

(4) We discussed an approximate formula for the bias and an exact formula for the mean square error (MSE), which were not provided by Worlund and Taylor.

(5) As an aid to planning studies, it can be noted that the bias is low when the probability of obtaining all tests positive is low. This can be seen from the expectation of $\hat{p}$ conditioned on not getting all tests positive. When all tests are positive, the estimator is 1.0 even though the actual value of p can be much lower.

Worlund and Taylor might have pointed out other potential uses for the methodology. For example, Dare (1977) and Cone and Moore (1981) described laboratory procedures for testing groups of mussels for parasitic copepods and groups of salmonids for pancreatic virus, respectively. These procedures lend themselves to the statistical methodology of group testing. Reviews of other applications can be found in Loyer (1983) and Hoenig (1981).

Finally, it should be noted that group testing can be generalized to more complicated models such as trinomial responses, bivariate binomial models, and testing with groups of variable size (Loyer 1983; Hoenig and Lawing, in prep.) — John M. Hoenig, *Minnesota Department of Natural Resources, Section of Fisheries, Box 12, Centennial Bldg., St. Paul, MN 55155, USA*, and William D. Lawing, *Department of Statistics and Department of Industrial Engineering, University of Rhode Island, Kingston, RI 02881, USA*.

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Reply

Group testing has indeed been around for many years, for enough years to become a standard procedure. Our work involved using basic elements found in probability textbooks to solve a practical problem; and our purpose in publishing was to make it available to others who might find it useful — not to announce "an invention." Statistical methodology, like the wheel, is useless if not widely available and put to practical use.

We agree that the paper contained an indadequate review of the literature. In fact it contained no review at all. It cited a textbook reference and one similar problem. It was presented as a note and not as a comprehensive paper on the subject.

We are pleased that few problems were found with the treatment of the subject and appreciate the constructive comments made by Drs Lawing and Hoenig. We look forward to their forthcoming paper. The subject is of importance to those who inspect and must certify that fish or fish products are free of certain infectious diseases.

A final point concerns the appropriate model referred to by Hoenig and Lawing. The binomial model is an approximation at best, since sampling is done without replacement. This is the reason we limited the method to cases in which the population is large relative to sample size, and *assume*, wrongly to some degree, that the disease incidence in the population remains constant during the sampling process. It seems clear that the hypergeometric model is appropriate, and especially important to use when sampling from small populations. — D. D. Worlund, *National Marine Fisheries Service, Northwest Alaska Fisheries Center, 2725 Montlake Boulevard East, Seattle, WA 98112, USA.*

BOOK REVIEWS/COMPTES RENDUS

The Biology of Crustacea — Environmental Adaptations. *F. J. Vernberg and W. B. Vernberg. Academic Press, New York, NY. 1983. 383 p. ISBN 0-12-106408. $67.*

This book is the eighth in a series devoted to discussion of all aspects of crustacean biology, with earlier volumes being devoted to systematics and biogeography; embryology, morphology, and genetics; neurobiology; neural integration and behaviour; internal anatomy and physiological regulation; pathobiology; and behaviour and ecology. The topic of discussion, environmental adaptations, was intended to bridge the gap between those volumes dealing in detail with the functional components of crustaceans and those dealing with ecological, taxonomic, behavioural, and applied subjects. Unfortunately, the goal to examine the dynamic interaction between an organism and its external environment in order to emphasize the adaptative significance of its responses has been poorly achieved.

Two problems are evident: first, the interaction of an organism with its external environment is obviously very complex, ranging from interactions with specific physical parameters to interactions with biotic competitors, predators, and prey. When this is expanded to include all crustacean species, the subject becomes so vast that it cannot be adequately dealt with by one volume of seven chapters. I would have thought that this most interesting subject could have been expanded to include a number of more clearly focused volumes in the overall series. For example, separate volumes could perhaps have dealt with how individuals or species respond to abiotic extremes and the invasion of new habitats (e.g. terrestrial, freshwater, etc.); how biotic interactions have influenced crustacean behaviour, morphology, and evolution; and finally, the significance of how variability of response and degree of adaptation between individuals within a population influence species ecology.

Among the seven chapters presented, three discuss interactions with the chemical environment (respiration (2) and chemical and osmotic regulation), two deal with life processes (feeding and reproduction), and two deal with adaptations to specific habitats (freshwater and terrestrial). The relatively heavy emphasis on crustacean interactions with the chemical environment reflects the editor's expertise in this field, but it is the reader's loss that a broader perspective could not have been presented.

The second problem is one common to series with contributions from many authors. Gaps, overlaps, and inconsistencies become unavoidable, and in a series of eight editors and almost 100 contributors, this deficiency is noticeably evident. Under the guise of discussing interactions and their adaptive significances, the chapters dealing with the chemical environment in particular seem redundant and often out of context. Discussion frequently reverts to description of control mechanisms rather than interpretation of response ability, and while most variables are referred to, they are often dealt with in an uninformative, token manner. For example, in F. J. Vernberg's chapter on respiratory adaptations, the section dealing with parasitism consists entirely of the following three sentences: "The metabolism of an organism parasitized by another species may be influenced. For example, when the coridean shrimp *Palaemonetes pugio* is infected by the isopod *Probophyrus pandalicola*, its metabolic rate is dramatically reduced (Anderson, 1975b). This response may reflect changes in lipid metabolism as a host response to parasitism."

Apart from demonstrating poor grammar and leaving much interpretation to the reader, it also illustrates the verbatim reporting style of this author. The published literature is acknowledged but there is little discussion of both the topic as a whole and the relevance of the cited material.

In contrast, I found the chapters on life processes and terrestrial adaptions well-organized and relevant, and for these chapters alone, I would recommend this volume. This series' concept of bringing together background material in a concise but complete perspective of various aspects of crustacean biology is one I strongly support, and I hope that future volumes can expand on how species are adapted to their environment. It is both the ability to adapt and the tolerance to change that determines a species' real evolutionary success, and much remains to be addressed.

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(R566)

Chironomidae of the Holarctic Region. Keys and Diagnoses. Part 1. Larvae. *Edited by Torgny Wiederholm. Etomologica Scandinavica. 1983. 457 p. ISBN 0105-3574. $73 (U.S.).*

A Review of the Genera *Doithrix* n. gen., *Georthocladius* Strenzke, *Parachaetocladius* Wülker and *Pseudorthocladius* Goetghebuer (Diptera: Chironomidae, Orthocladiinae) (Supplement No. 20), *Ole A. Saether and James E. Sublette. Entomologica Scandinavica. 1983. 100 p. $19 (U.S.).*

A Catalogue of Chironomid Genera and Subgenera of the World Including Synonyms (Diptera: Chironomidae) (Supplement 17). *P. Ashe. Entomologica Scandinavica. 1983. 68 p. $15 (U.S.).*

The long-awaited *Chironomidae of the Holarctic Region* (orders were being taken in 1981) is the first publication in which identification keys, descriptions, and illustrations for all the larval chironomid genera have been assembled in a single volume. Considering the extensive material scattered throughout the literature, this is indeed a welcome effort. The format and layout are clear and easy to use. The volume consists of 10

separate papers preceded by a foreword, and all the references amalgamated at the end. Treating each subfamily as a separate paper, yet maintaining the high quality and consistency of diagrams and descriptions throughout the book, enables both beginners and experts to quickly review each section for content. The title pages at the beginning of each paper are especially useful, providing concise information on each subfamily, a clear indication of the content of the paper, and addresses of the author(s) to encourage exchange of information and specimens.

As a state-of-the-art work it naturally has several problems that may impede some biologists, particularly beginners. Perhaps because the information was assembled from existing literature and not from recently examined specimens, some Orthocladiinae and Tanypodinae genera in my collection, verified by one of the authors, could not be identified using these keys. Generally, however, the descriptions and the drawings will clarify any problems.

The most confusing section is the essentially one-page key to the subfamilies. Because all other identifications hinge on correct subfamilial identification, this paper could be greatly expanded to include an entire array of key characteristics such as those used in tabular keys. Although the dichotomous keys work well in the more lengthy generic identifications, a tabular key would be less likely to lead to error while providing more justification for the eight subfamilial divisions.

Readers are referred to the morphological terminology outlined by Saether (1980) but the inclusion of a precis of this valuable contribution would have enhanced this book, especially since the terms are used extensively in each section. This drawback could have been overcome, perhaps, if the excellent drawings were labelled in more detail, pointing out specific characters used in the key on the figure itself.

Notwithstanding the minor problems, this book is highly recommended to all those working with chironomid larvae. The keys work relatively well for most genera. The descriptions, which also contain some ecological and distributional information and keys to species where possible, include most of the information necessary to confirm identifications. Users should bear in mind that this is a first attempt at consolidation of a vast amount of information, and at least one of the authors (D. R. Oliver, pers. comm.) has welcomed suggestions and encouraged specimen exchange for a possible future review.

The publication by Saether and Sublette lives up to the high standards of the previous reviews of chironomid genera and species by these authors. The authors present a concise introduction with keys to the males, pupae, and larvae of the four genera discussed, followed by detailed descriptions of each specific life stage. Keys to species in latter parts of the publication work fairly well, although identifying the larvae of *Pseudorthocladius* is a problem. This appears to be the result of quoting from the literature without reexamining the actual specimens. This genus still awaits definitive revision. It is nice to see so many well-executed and well-drawn illustrations to reinforce the descriptions, along with several SEM photomicrographs of various structures. This relatively error-free presentation will certainly be of benefit to all those who identify chironomids.

The long-needed publication of Ashe carefully and concisely lists the chironomid genera and subgenera, including synonyms. The introductory section is particularly well written, precisely describing the purpose, methods, and format. The genera and subgenera are listed alphabetically, the subfamilial classification being indicated with the synonymies. The very tedious task of categorizing 524 recent genus-group names has been well executed. All known genera are included and decisions on taxonomic status are justified. This work consolidates and clarifies the widely dispersed but voluminous recent chironomid literature.

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(R569, R570, R571)

Control Processes in Fish Physiology. *Edited by J. C. Rankin, T. J. Pitcher, and R. Duggan. Wiley Interscience Publications, New York, NY. 1983. 298 p. $39.95.*

Amongst vertebrates, fish are probably rivalled only by a few mammalian species as far as physiological research interest is concerned. This popularity stems from their species diversity and extensive adaptive radiation (over 400 families living in almost every kind of aquatic habitat), their economic importance as food, their value and interest to sportsfishermen and aquarists, and their strategic position in vertebrate phylogeny. In the last decade this research interest has intensified greatly. This has been true especially for a few semidomesticated teleost species and has developed largely in response to expansion in the field of aquaculture (fish farming) and the recognition of environmental encroachment and waterborne pollutants and their potentially devastating effects on wild fish populations. The resulting voluminous literature represents a source of frustration. Most of us focus our research efforts on one organ system (e.g. olfactory system or reproductive system or, in extreme cases, even on a single endocrine gland). We can usually keep up with the literature in our speciality but tend to fall behind in our general appreciation of how the rest of the fish works. Some assistance is provided through already-published reviews and by *Fish Physiology*, the multivolume treatise published by Academic Press which covers most facets of the topic. However, its machinery is ponderous. The first three volumes of *Fish Physiology* were published 15 years ago and only limited aspects from those early volumes have been rereviewed in later volumes. Furthermore, related to their exhaustive treatment, certain chapters in *Fish Physiology* tend to provide a catalogue rather than a synthetic definition of the current pulse of the topic.

Control Processes in Fish Physiology comprises a single pocket-size volume (249 text pages), which evolved from the proceedings of the 3rd International Symposium on Fish Physiology held at Bangor, Wales, in September 1981. During the Symposium it was decided that instead of attempting to publish all material presented at the meeting, selected speakers (75% from the United Kingdom) should be invited to "summarize from a wider perspective how some of the major processes in fish physiology are controlled." The aim of the 12-chapter volume was to provide "a useful introduction to the senior undergraduate and post-graduate student of Zoology or Biology, as well as providing reviews for the specialist physiologist and those with interest in applied fish physiology."

The approach was directed deliberately towards whole-fish physiology, largely ignoring control at the biochemical or genetic level. The limits of the physiologic spectrum actually

covered extend from "Pancreatic Control of Metabolism" (Ince) at the biochemical fringe to "Synthetic Chemicals and Pheromones in Homing Salmon" (Hasler), "Hormones and Reproductive Behaviour in Teleosts" (Stacey), and "Hormones and Agonistic Behaviour in Teleosts" (Munro and Pitcher) at the ethological fringe. The other chapters deal with the "Autonomic System" (Nilsson et al.), "Digestion and Control of Gastrointestinal Motility" (Holmgren et al.), "Control of Respiration and Circulation" (Butler and Metcalfe), "Osmoregulation and Control of Kidney Function" (Rankin et al.), "Integration and Control by the Central Nervous System" (Guthrie), "Oocyte Developmental Patterns" (de Vlaming), "Control of Trout Reproduction" (Scott and Sumpter), and "Control of Reproduction in Elasmobranch Fish" (Dodd et al.).

In comparison with many conference proceedings, I found the result refreshing, stimulating, and useful. Hopefully this procedure will be repeated after the 4th international meeting of this group. With hindsight the next version might be published with less delay. However, despite the 2-year lag between the conference and the publication it is to the credit of most authors that presentations have been updated with liberal sprinklings of 1982 and even 1983 references. References, by the way, are presented in full as one list (38 pages) at the end of the volume, together with both species and subject indices.

The chapters in most cases explore their individual topics to about the same depth and represent easily digestable quanta. In many instances authors have emphasized data from their own laboratory. In view of the origin of the book this is legitimate and in most cases does not detract from the intent to provide an overview. Some chapters may not be that useful to the specialist in his or her particular field, as more exhaustive and up-to-date reviews may already be available. However, most chapters will be useful to the student or researcher who already has a marginal grasp of the subject and who wishes to find out quickly what is happening in that area. I have found the book of value in preparing course lectures and in gaining a better general insight as to how fish work. One stated goal was to aid research in applied physiology, particularly fisheries and fish farming. The chapter most likely to be of value in this regard, both because of its subject matter and style of treatment, is that of Scott and Sumpter on "Control of Trout Reproduction." However, even on this topic there is still a large gap between research findings and practical application and it is unlikely that this goal will be accomplished by the current volume.

The book can best be summarized as providing a series of minireviews on major but selected aspects of fish physiology. The goal was clearly to establish a holistic treatment of how fish work. Such a broad biological perspective is highly fitting in a volume dedicated to Professor J. M. Dodd on the occasion of his retirement from the Lloyd Roberts Chair at the University College of North Wales.

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(R560)

BOOKS RECEIVED/LIVRES REÇUS

Making and Managing a Trout Lake. *Rupert Barrington. Fishing News Books Ltd., England. 1983. 136 p. £5.00. ISBN 0-85238-126-3.* For the benefit of land owners, managers of freshwaters, anglers, and nature lovers, the volume presents a detailed account of what is involved in building and managing a lake, with emphasis on trout fishing. [R565]

Scallop and Queen Fisheries in the British Isles. *James Mason. Fishing News Books Ltd., England. 1983. 136 p. £6.90. ISBN 0-85238-128-X.* The book deals in detail with life history, breeding and behavior, catching methods, and development of the scallop and queen fisheries. As fishing has expanded, attention has turned to stock protection and the possibility of farming pectinids or replenishing natural stocks. [R573]

Engineering, Economics and Fisheries Management. *Gordon C. Eddie. Fishing News Books Ltd., England. 1984. 112 p. £6.50. ISBN 0-85238-127-1.* The book draws attention to aspects of everyday life in the fishing industry, and to economic and practical constraints on development that are not often appreciated, in the hope that they will be taken into account when schemes of fisheries management or government support are being devised. [R574]

Vibrios in the Environment. *Edited by Rita R. Colwell. John Wiley & Sons, Inc., New Jersey. 1984. 634 p. $45.00 (U.S.). ISBN 0-471-87343-8.* Over the past 10 years the Vibrionaceae have become increasingly interesting to microbiologists. The book consolidates, for the first time, information on epidemiology, serology, pathogenesis, molecular genetic aspects, and ecology of pathogenic vibrios and related organisms as well as their isolation, enumeration, and identification, and implications for the seafood industry. [R575]

Problemes d'écologie. Ecosystèmes limniques. *M. Lamotte et F. Bourliere. Masson, Paris. 1983. 264 p. 225 F. ISBN 2-225-80011-1.* In recognition of the fact that studies on entire ecosystems are still rare, the book treats five lake ecosystems studied by French hydrobiologists. [R576]

Small-Scale Fisheries of San Miguel Bay, Philippines: Economics of Production and Marketing. *Ian R. Smith and Antonio N. Mines. ICLARM, Manila, Philippines. 1982. 143 p. $12.00 (U.S.) surface and $25.00 (U.S.) airmail. ISSN 0115-5547.* Small-scale fisheries of San Miguel Bay: economics of production and marketing. [R577]

Small-Scale Fisheries of San Miguel Bay, Philippines: Social Aspects of Production and Marketing. *Edited by Conner Bailey. ICLARM, Manila, Philippines. 1982. 57 p. $8.00 (U.S.) surface and $14.00 (U.S.) airmail. ISSN 0115-5547.* The report is one of four emanating from a research project undertaken to provide basic biological and socio-economic information on the fisheries of the Bicol Region. It analyzes social linkages among fishing communities of San Miguel Bay, attitudes toward fish production, processing, and marketing, economic role of women and children, variation in sharing systems by gear types, and socioeconomic aspects of the marketing system. Data gathered from interviews with 641 fishing households are presented and supplemented by participant observation. [R578]

Nitrogen in the Marine Environment. *Edward J. Carpenter and Douglas G. Capone. Academic Press Inc., New York, NY. 1983. 900 p. $59.00 (U.S.). ISBN 0-12-160280-X.* Global nitrogen cycling in the sea has recently come under heightened scrutiny, as it has been reported as the primary limiting nutrient in coastal waters. The editors have gathered together papers on the role of microbes in nitrogen transformations, with consideration of higher tropic levels. Nitrogen cycling in various ecosystems within the marine environment is also examined. [R579]

Evolutionary Ecology of Neotropical Freshwater Fishes. *Thomas M. Zaret. Dr. W. Junk bv Publishers, The Hague, The Netherlands. 1984. 174 p. $56.00 (U.S.). £37.00. ISBN 90-6193-823-6.* This conference proceedings is reprinted from *Environmental Biology of Fishes* 9 (2), 1983, with addition of three more papers from the conference and synopses in Spanish and Portuguese. [R580]

Potential for Viable Aquaculture Endeavours in British Columbia. *Envirocon Limited, Science Council of British Columbia, Richmond, B.C. 1984. 98 p. $12.00 (Cdn.).* The Science Council of British Columbia commissioned a study by Envirocon Ltd. to discover instances in which research could help overcome some of the problems being experienced by the aquaculture industry and to identify those aquacultural activities that are likely to have positive economic returns for the province within the next 5–10 years. [R581]

Advances in Assessment of World Cephalopod Resources. *J. F. Caddy. Food and Agriculture Organization of the United Nations, Rome. 1983. 452 p. ISBN 92-5-001431-7.*

Some of the more promising approaches in assessing cephalopod resources are presented in 11 papers and should be of value to research workers entering this field. [R582]

Fisheries Acoustics. A Practical Manual for Aquatic Biomass Estimation. *K. A. Johannesson and R. B. Mitson. Food and Agriculture Organization of the United Nations, Rome. 1983. 240 p. ISBN 92-5-101449-3.* [R583]

FAO Species Catalogue. Vol. 2. Scombrids of the World. *Bruce B. Collette and Cornelia E. Nauen. Food and Agriculture Organization of the United Nations, Rome. 1983. 137 p. ISBN 92-5-101381-0.* The present volume is the second in a series of species catalogues that will comprise a worldwide annotated and illustrated inventory of aquatic food species FAO will build up. The report covers the 49 known species of scombrids, including keys to genera and species, illustrated glossary, distribution maps, list of scientific and common names, and information on habitat, biology, and fisheries. [R584]

CORRECTIONS TO RECENT PUBLICATIONS
CORRECTIONS SUR RÉCENTS PUBLICATIONS

VOLUME 40, No. 10 — article by M. P. Weinstein: *Population dynamics of an estuarine-dependent fish, the spot* (Leiostomus xanthurus), *along a tidal creek–seagrass meadow coenocline*.

Page 1633, Abstract line 13 (French line 16): "...21.8 kcal (91342 J)·m^{-2}·d^{-1}. This figure is over six times greater..." should read "...239 cal (1000 J)·m^{-2}·d^{-1}. This figure is over 80 times greater..." ("...Ce chiffre est 80 fois supérieur..."). The Contribution No. should read "1141."

Page 1637, left column, lines 14 and 15: "...0.382 g·m^{-2}, or 1960 cal (8212 J)·m^{-2}" should read "...4.193 g·m^{-2}, or 21 550 (90 167 J)·m^{-2}".

VOLUME 41, No. 3 — note by R. J. Maguire, P. T. S. Wong, and J. S. Rhamey: *Accumulation and metabolism of tri-n-butyltin cation by a green alga,* Ankistrodesmus falcatus.

Page 537, left column, last line: "($t_{1/2}$ 89 d)" should read "($t_{1/2} > 89$ d)".

Page 538, right column, second-last line: "Sn^{2+}" should read "Sn^{4+}".

ANNOUNCEMENTS/AVIS

The Eleventh Annual Toxicity Workshop will be held in Vancouver, British Columbia, November 13–15, 1984. The workshop will include a plenary session on the effects of mine wastes on aquatic systems, contributed and invited papers, and poster sessions. For further information contact: Dr. Glen H. Geen, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C. V5A 1S6.

Le 11e Atelier annuel sur la toxicité aquatique aura lieu à Vancouver (Colombie-Britannique), du 13 au 15 novembre 1984. L'atelier comprendra une séance plénière traitant des effets des stériles miniers sur les systèmes aquatiques ainsi que des présentations d'exposés spontanés et sollicités ainsi qu'une exposition d'affiches. Pour renseignements, veuillez contacter : M. Glen H. Geen, D.Ph., Département des sciences biologiques, Université Simon Fraser, Burnaby (C.-B.) V5A 1S6.

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

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Determination of corticosteroids in fish plasma by high performance liquid chromatography: evaluation of the method using striped bass (*Morone saxatilis*) **R. B. MacFarlane**

Variable gut residence time: problems in inferring feeding rate from stomach fullness of a mysid crustacean **P. A. Murtaugh**

Selective exploitation of capelin (*Mallotus villosus*) eggs by winter flounder (*Pseudopleuronectes americanus*): capelin egg mortalities, and contribution of egg energy to the annual growth of flounder **K. T. Frank and W. C. Leggett**

Zooplankton and potential fish production in Lake Ontario **U. Borgmann, H. Shear, and J. Moore**

Lethal and sublethal toxicity of drilling fluids to larvae of the American lobster, *Homarus americanus* **J. G. S. Derby and J. M. Capuzzo**

Influence of temperature and light on rates of inorganic nitrogen transport by algae in an arctic lake **S. C. Whalen and V. Alexander**

Pacific salmon (*Oncorhynchus*) migrations: orientation versus random movement **T. P. Quinn and C. Groot**

Generalized Stock Reduction Analysis **D. K. Kimura, J. W. Balsiger, and D. H. Ito**

Statistical inference in life-table experiments: the finite rate of increase **P. J. Rago and R. M. Dorazio**

Selection of external tags for marking Atlantic herring (*Clupea harengus harengus*) **B. S. Nakashima and G. H. Winters**

Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*) **R. A. Myers**

Extracellular protease, extracellular haemolysin, and virulence in *Aeromonas salmonicida* **J. L. Hackett, W. H. Lynch, W. D. Paterson, and D. H. Coombs**

Influence of chlorine on the susceptibility of striped bass (*Morone saxatilis*) to *Vibrio anguillarum* **F. M. Hetrick, L. W. Hall, Jr., S. Wolski, W. C. Graves, B. S. Roberson, and D. T. Burton**

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Comparisons of growth in weight of temperate and tropical marine fish counterparts **R. R. C. Edwards**

Evaluation of acid-insoluble ash as an indicator of feed digestibility in rainbow trout (*Salmo gairdneri*) **J. L. Atkinson, J. W. Hilton, and S. J. Slinger**

Growth and gonadal development in triploid landlocked Atlantic salmon (*Salmo salar*) **T. J. Benfey and A. M. Sutterlin**

Perspectives

Multiattribute analysis and the concept of optimum yield **M. C. Healey**

Book reviews/Comptes rendus

Aquatic toxicology (edited by J. O. Nriagu) **J. B. Sprague**

The chartmakers — A history of nautical surveying in Canada (Stanley Fillmore and R. W. Sandilands) **G. Castle**

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